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VARIATION OF FUNGI DUE TO ENVIRONMENT[1]

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(WITH THIRTY-SEVEN FIGURES)

The effects of environment, climatic condition, soil fertility, the presence of unusual chemicals, the water relation, and what not, upon the form and characters of seed plants, are well known to the plant physiologist, and have been the subject of numerous studies. These factors are even utilized by the practical man to bring about desired variation.

That fungi vary similarly will not be doubted by any who have had to do with fungi in artificial cultures. The kind and degree of such variation, we dare say, will be a surprise to any who have not made special study of this subject.

Our knowledge of the seed plants, owing to man's long acquaintance with them, their larger size, and comparative stability, is considerable; yet even with them the limiting of genera, species, varieties, etc., presents difficulty, if we may judge from the rich literature upon phanerogamic taxonomy. The fungi, because of their immense number of species, variety of forms, minuteness, paucity of distinguishing characters, complexity of life-history (mostly unknown), peculiar biologic host relations (almost entirely unknown), and because of man's short acquaintance with them and their unknown but apparently vast range of variability, present as yet baffling problems of relationship and classification.

The object of the present paper is to call attention to the kind and degree of environmental variation found in a few species of fungi that have been studied by the authors during the past four or five years,

[1] Read in part at the Baltimore meeting of the Botanical Society of America, December, 1908.

and in some instances to analyze the causes of these variations, to the end that the factor of environmental variation may be more clearly recognized as a problem of mycological taxonomy.

We shall consider these variations under the causes that produce them.

I. Density of colonies

SEPTORIA PETROSELINI DESM. VAR. APII BR. & CAV., FROM CELERY

This fungus, when plated so that the spores lay thinly scattered, produced colonies which were ultimately black, 1 to 2^{mm} in diameter,

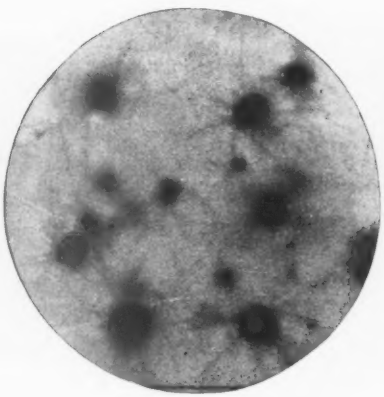

FIG. 1

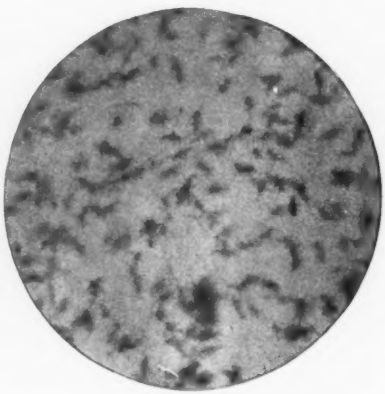

FIG. 2

FIG. 1. *Septoria Lycopersici* Speg., showing formation of normal pycnidia on portion of thinly sown plate culture.—FIG. 2. *Septoria Lycopersici* Speg., showing absence of pycnidia on thinly sown portion of plate culture; magnification same as in *fig. 1*.

with pycnidia of normal character. If plated so that the spores lay in large numbers per square centimeter, it produced colonies which reached a size of only about 0.5^{mm} and became ultimately black, containing ordinary pycnidia, bearing spores in the normal way. When plated so that there were still more spores per square centimeter, the colonies never became black and no pycnidia were produced; but on the contrary, multitudes of spores were borne uncovered, in clumps upon simple hyphae.

SEPTORIA LYCOPERSICI SPEG., FROM TOMATO

Spores from pure culture were plated in 4 per cent. pea agar in various dilutions.

One plate developed 5 to 6 colonies per square millimeter and each colony proceeded to normal pycnidial development. Another plate developed 21 to 23 colonies per square millimeter, and all proceeded to form naked conidia with no indication of pycnidia. Portions of these two plates are represented by photomicrographs (*figs. 1, 2*). Drawings of the naked spores showing the detail of their formation are given in *fig. 3*. Occasionally plates with as many as 30 colonies per square millimeter were found with both pycnidia and naked spores.

Pycnidia not visible at the fifth day may be well formed by the eighth day and extrude masses of pink spores about the twenty-first day. Occasionally pycnidia are well developed on the fourth day. When naked spores develop they normally appear a few days later than do pycnidia, e. g., a plate thinly sown January 12, 1907, gave many pycnidia on January 15; while a thickly sown plate, under conditions otherwise precisely parallel, did not give naked spores until January 22. This Septoria forms a typical determinate colony, i. e., even with unlimited room, it proceeds only to a certain size of development.

FIG. 3.—Mode of formation of naked spores under influence of crowded culture.

SEPTORIA CONSIMILIS E. & M., FROM LETTUCE

When sown thinly, colonies reached a size of 2 to 3^{mm} in diameter; when sown thickly, they became no more than 0.2^{mm} in diameter. There was no interference with color development or formation of pycnidia by thick sowing with this species.

With two of these septorias, thick plating, other conditions being the same, so changed their character that not only would the species be considered as different, but the fungus would be shifted from the order Sphaeropsidales to the order Hyphomycetales (Hyplaesa of SACCARDO).

A similar change of habit is well known in the genus Fusarium, which in culture, crowded or not, often abandons acervulus formation, thus changing its systematic position from the Tuberculariaceae to the Mucedinaceae. The genera Colletotrichum and Gloeosporium similarly abandon acervulus formation and thus suffer still greater taxonomic disturbance by moving from the Melanconiales to the Hyphomycetales.

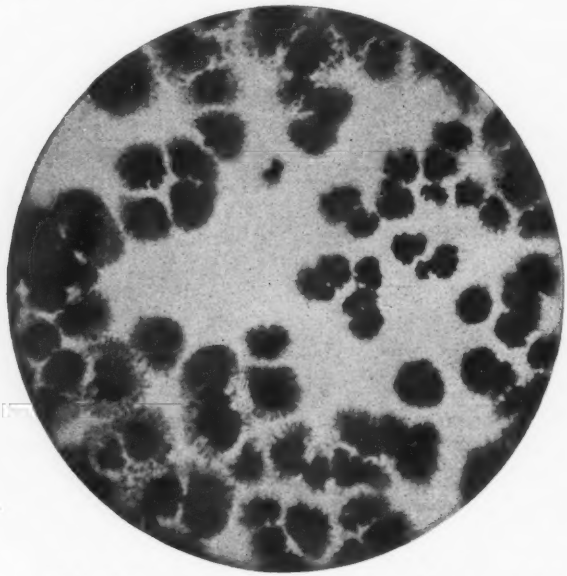

FIG. 4.—*Volutella fructi* S. & H., showing colonies on thinly sown plate culture.

ASCOCHYTA CHRYSANTHEMI STEVENS, FROM CHRYSANTHEMUM

This fungus was plated January 12, 1907. Myriads of pycnidia were present four days later. Thick plating caused no inhibition of pycnidial formation, no naked spores, and no constant effect upon the number of pycnidia produced.

VOLUTELLA FRUCTI S. & H., FROM APPLE

Thinly sown, the colonies were large, of indeterminate growth, showing dark centers with pale borders (*fig. 4*). Thickly sown, growth was inhibited and these characters lost (*fig. 5*).

SPERMOEDIA PASPALI FRIES, FROM PASPALUM[2]

Spores of this fungus were sown January 19, 1907, in plates giving colony densities of 90, 54, 30, 14, and 1 per square millimeter.

At all of these densities germination was practically 100 per cent. and growth proceeded equally in all plates during the early stages. On February 11 it was noted that all colonies which came nearly in

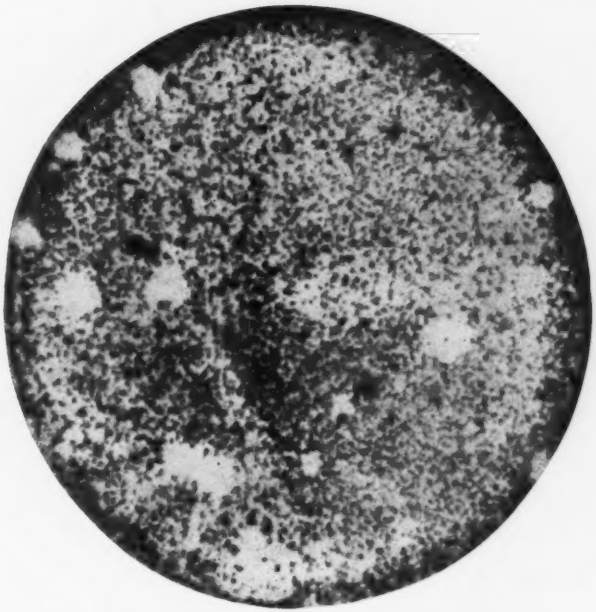

FIG. 5.—*Volutella fructi* S. & H., showing effect of thick sowing.

contact were sporing. Growth then stopped. In the plates bearing only one spore per square millimeter the colonies continued to enlarge slowly and to produce many spores in the central portion, though remaining white, not attaining the usual yellow color. Deep colonies appeared like the superficial, but bore no spores. On February 7 the colonies on thin plates (1 per square millimeter) had attained a

[2] Later study has shown this to be the imperfect stage of an undescribed species of Claviceps, which we shall describe in a subsequent paper.

diameter of 1.5^{mm}. Some of these colonies transferred to tubes continued to enlarge, became tubercular, and developed a yellow center 3 or 4^{mm} in diameter. The whole colony often reached 1^{cm} in diameter. Sister colonies left in the plate (1 per square millimeter) failed so to develop, and it is evident that at even this density normal development is not attained.

The colony is indeterminate in growth, and in plates its size is limited by the presence of adjacent colonies.

SUMMARY REGARDING THE DENSITY FACTOR

This factor produces different effects with the different species. It may inhibit pycnidial formation, resulting in naked spores; it may cause failure to develop color; it may limit the size of the colony; it may be without effect.

There are many paired species of the imperfect fungi agreeing closely, except in the presence or absence of one character. These pairs often occur upon the same host, e. g., *Septoria Lycopersici* Speg. and a Cylindrosporium on the tomato; *Cylindrosporium Chrysanthemi* E. & D. and *Septoria Chrysanthemi* Cav. on the cultivated chrysanthemum.[3] Many other instances could be cited. The lack of fixity of such a structure as even the pycnidium throws doubt upon the validity of such species as these and indicates the necessity of close comparative study.

II. Density of mycelium: zone formation

The formation of concentric zones is by many fungi one of the most conspicuous characters shown in culture. These zones may be

[3] VOGLINO, P., Diseases of cultivated chrysanthemums. Malpighia **15**:329–341. 1902. (Exp. Sta. Rec. **14**:777.)

HALSTED, B. D., Chrysanthemum leaf spot. Amer. Florist **10**:263. 1894. (Exp. Sta. Rec. **6**:311.)

BEACH, S. A., Leaf spot of chrysanthemum. Report of Horticulturist, N. Y. Exp. Sta. Rept. **1892**:557–560.

HALSTED, B. D., Report of fungus disease of plants. N. J. Exp. Sta. Report **1891**:233–340.

SACCARDO, Syll. Fung. **2**:542, *n.* 3497, 3498, 3757.

TUBEUF & SMITH, Diseases of plants 478.

Year Book U. S. Dept. Agr. **1906**:507.

New York Agr. Expt. Sta. Rept. **14**:529.

New Jersey Agr. Expt. Sta. **1894**:361.

due to any one of many structural characters of the colony; to varying density of spore massing, grouping of pycnidia, mycelial branching, color, etc. It is a frequent phenomenon in nature in the fairy rings of the toadstools, the concentric markings of many leaf spots, fruit rots, etc. These effects have been attributed to various causal agencies, to light relation,[4] to nutrients,[5] to agencies other than light, probably food, to resting periods (HEDGECOCK, *l. c.*), and to mycelial crowding.[6]

ASCOCHYTA CHRYSANTHEMI STEVENS

With the fungus in question the fact that the zones are not due to light or temperature relations is apparent from the fact that they do not coincide with the fluctuations of these two factors (*fig. 6*). In the colony shown, which is that of a plate culture kept at room temperature, there was daily change from warm to cool, light to dark; yet the number of rings does not coincide with the number of these changes; moreover, zones were produced in precisely the same way on plates kept constantly in the dark as on plates kept all of the time in the light, and still the same on plates kept three days in the dark and then three days in the light.

Microscopic examination shows that with this fungus the dark zone is due to a larger number of mycelial filaments, the light zone to a smaller number of threads, as is shown diagrammatically in *fig. 7*. It seems that with this fungus the dense crowding of the filaments, resulting from their repeated branching, inhibits growth either by the products of metabolism or exhaustion of nutriment. There is then a period of quiescence, followed by onward growth of a few scattered hyphae. As these outgrowing hyphae reach beyond the inhibiting influence, they branch repeatedly, until a new dense zone

[4] MOLZ, EMIL, Ueber die Bedingungen der Entstehung der durch *Sclerotinia fructigena* erzeugten Schwarzfaule der Aepfel. Cent. Bakt. **17**²:175.

HUTCHINSON, H. B., Ueber Form und Bau der Kolonieen niederer Pilze. Cent. Bakt. **17**²:602.

HEDGECOCK, G. G., Zonation in artificial culture of Cephalothecium and other fungi. Rept. Mo. Bot. Garden **17**:115–117. *pls. 13–16.* 1906.

[5] MILBURN, THOS., Ueber Aenderungen der Farben bei Pilzen und Bakterien. Cent. Bakt. **13**²:257.

[6] ISTVÁNFFI, GY. DE, Études microbiologiques et mycologiques sur le rot gris de la vigne. Ann. Institut Cent. Ampél. Roy. Hongrois **1905**:183.

is formed. This process is repeated indefinitely. The rapidity of succession of zones is dependent solely upon the relation which rapidity of branching bears to rapidity of increase in length. Slow lineal

FIG. 6.—*Ascochyta Chrysanthemi* Stevens; plate culture showing that the formation of zones is not coincident with diurnal changes; ink marks show growth for three consecutive days.

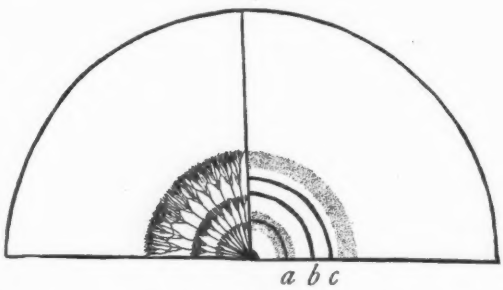

FIG. 7.—Diagram showing, at right, the zones (stippled) and diurnal marks; at left, theoretical expression of cause of zonation.

growth and much branching gives many narrow zones, rapid lineal growth with infrequent branching causes few broad zones.

Sclerotinia Libertiana Fuckel, from lettuce

Zonal sclerotial formation is exhibited by this fungus (*fig. 8*). That this phenomenon may be attributed to crowding of the mycelium is indicated by the fact that adjacent colonies form more sclerotia at their points of contact (*fig. 9*).

Fig. 8.—*Sclerotinia Libertiana* Fuck., showing zonal formation of sclerotia on corn-meal culture.

SUMMARY REGARDING DENSITY OF MYCELIUM

Zone formation in *Ascochyta Chrysanthemi* is due to crowding of mycelium, not to light or heat relation. A similar conclusion was reached by Istvánffi[6] regarding the very striking zones shown by Sclerotinia. The same cause may apply also with *Daldinia concentrica* and many other fungi of similar structure.

III. Chemical relations

Chemical relations have been studied with eleven fungi, the fungus being usually grown in agar with varying nutrients added. Occasionally other media were used. A chemical base agar (CBA) was

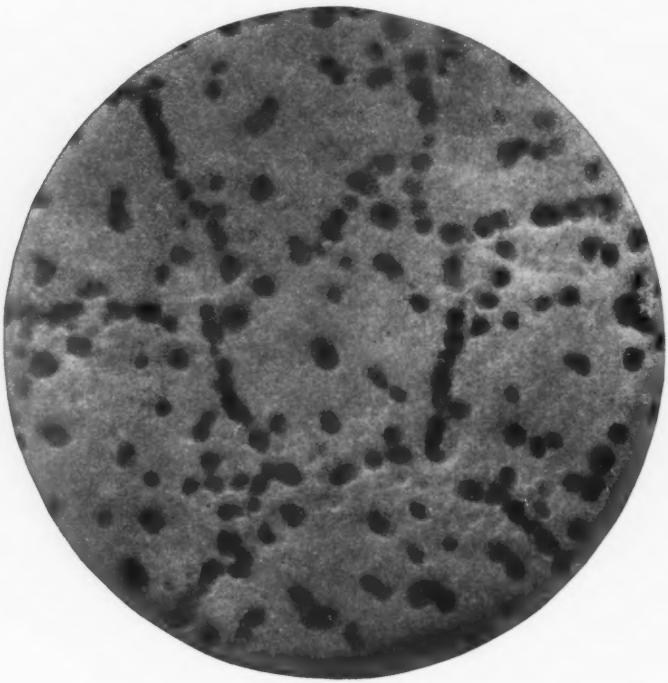

FIG. 9.—*Sclerotinia Libertiana* Fuck., showing the formation of sclerotia in greater abundance where adjacent colonies come in contact.

made of the following proportion (grams); water 1000, di-potassium phosphate 2.5, magnesium sulfate .01, calcium chlorid .01, sodium chlorid 2.5, potassium sulfate 2, agar 15. To 100^{cc} of this chemical base agar were added the following materials (grams) singly or in varying combinations: ammonium lactate 0.5, sodium asparaginate 0.25, glucose 1, starch 1. The tests were usually made in both plate and tube cultures.

VOLUTELLA FRUCTI S. & H., FROM APPLE

This fungus, when sown thin, forms large indeterminate colonies, often with numerous scattered tubercular blotches (*fig. 10*).

On pure agar and CBA the colonies were pale, mycelium hyaline, black tubercles very sparse.

On pea agar, black tubercles were much more abundant, otherwise as on pure agar.

On CBA+sodium asparaginate, black tubercles were still more numerous.

On CBA+sodium asparaginate+starch, black tubercles were more numerous than in any of the above, and the colony was black (*fig. 11*).

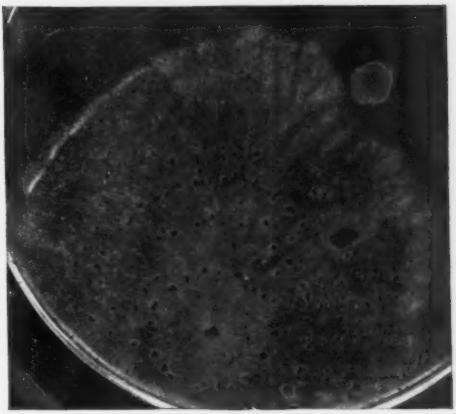

FIG. 10.—*Volutella fructi* S. & H.; colony on pea agar showing tubercular blotches, some of them in concentric rings; mycelium nearly hyaline, due to lack of carbohydrates.

On CBA+sodium asparaginate+glucose, black tubercles were still more numerous, so many as to be contiguous, and the whole colony was densely black.

On gelatinized starch, and starch+Uschinsky's solution, the mycelium was black and some digestion of the starch was observed.

On none of the above media were spores formed, but on sterilized apple twigs spores were produced in abundance.[7]

The differences here noted upon these different media are sufficient to alter entirely the general appearance and to shift the fungus from the Tuberculariaceae-Dematiae to the Tuberculariaceae-Mucedinae.

CONIOTHYRIUM FUCKELII SACC., FROM APPLE

This fungus when growing upon a medium rich in starch becomes black in its peripheral layer. Glucose fails to produce the same

[7] N. C. Agric. Exp. Sta. Bull. 196. June, 1907.

result. The mycelium is hyaline when on pea agar, but tawny on apple agar.[8]

SEPTORIA PETROSELINI VAR. APII, FROM CELERY

This fungus fails to produce naked spores when sown thickly on celery agar though it does so under similar conditions when upon lettuce agar.

COLLETOTRICHUM CARICA S. & H., FROM FIG

This fungus upon the different media used showed striking differences in: number of setae, varying from none to abundant; number of spores, varying from few to many; color, varying from pale to almost black.

FIG. 11.—*Volutella fructi* S. & H.; two black colonies upon CBA + sodium asparaginate + starch.

On CBA growth was scant; acervuli small, setae absent.

On CBA+ammonium lactate and CBA+sodium asparaginate, growth was about as in CBA, except that numerous black setae were present.

On CBA+ammonium lactate+ starch, the acervuli were larger, more numerous, with numerous large black setae.

On CBA+sodium asparaginate+ ammonium lactate, there were a few setae.

On CBA + sodium asparaginate + glucose, black setae were numerous.

EPICOCCUS SP., FROM APPLE AGAR IN PETRI DISHES

This fungus on pure agar and CBA was colorless. On CBA + starch or CBA+glucose, there was much richer mycelial development, which moreover took on a rich yellow color that in spots turned to

[8] N. C. Agric. Exp. Sta. Bull. 196:51.

pink. Sometimes black spots developed on the first of these media but not upon the second. This fungus shows strikingly the differentiating value of starch and glucose for fungus culture.

Upon apple agar still another character developed, a rich golden color of the abundant, floccose, matted, aerial hyphae. This reaction is fully as striking as the familiar rose color produced by certain species of Fusarium.[9]

With this fungus we have absence of color in agar and CBA, but rich coloring, of varying hues, in the presence of carbohydrates and upon apple agar.

PHYLLOSTICTA SP., FROM APPLE AGAR IN PETRI DISHES

This fungus grew faster on agar than on CBA, formed pycnidia sparsely on agar and not at all on CBA.

With sodium asparaginate added the mycelium became very dense, with considerable aerial development, remained colorless, and produced few pycnidia, and these visible only with the two-thirds objective. The presence of glucose led to exceedingly profuse pycnidial development, while on starch the growth was as with CBA+sodium asparaginate, showing again the ability to utilize glucose but not starch.

ALTERNARIA SP., FROM LAWSON CARNATION

This fungus, the cause of an apparently undescribed carnation disease which will be the subject of a subsequent paper, was isolated during October, 1908. There were striking differences in the color of the colony upon different media, varying from merely hyaline to dense black. The size and color of the spores were also so modified as to give much more than what is usually regarded as a specific difference.

On pure agar, CBA, CBA+ammonium lactate, CBA+sodium asparaginate, and upon CBA+ammonium lactate+sodium asparaginate, the mycelium was colorless and the colony correspondingly colorless; while upon CBA+sodium asparaginate+starch and CBA +sodium asparaginate+glucose, the mycelium was very dark, more profuse, more freely branched, and the colony therefore of an entirely different aspect.

[9] BESSEY, ERNST, Ueber die Bedingungen der Farbbildung bei Fusarium. Inaug. Diss. Halle. 1904.

Spore formation proceeded sparingly, though evenly and regularly, upon pure agar, CBA, CBA+ammonium lactate, CBA+sodium asparaginate, CBA+sodium asparaginate+ammonium lactate; but very abundantly upon CBA+sodium asparaginate+starch and upon CBA+sodium asparaginate+glucose. Here the sodium asparaginate seems not to furnish the carbon in sufficiently available form, though starch or glucose do so to nearly equal extent.

The size, color, and septation of the spores were also greatly influenced by the medium. From carnation-agar plates the spores measured 16 to 52 μ long by 6 to 13 μ thick, bearing 0 to 3 longitudinal septa and three to seven transverse septa; while from the live carnation leaf the spores were 26 to 123 μ long by 10 to 20 μ thick, bearing 1 to 9 or often numerous longitudinal septa and 3 to 15 transverse septa. It is seen that the spores are approximately twice as long, twice as thick, of darker color, and with many more septa in each direction upon the natural medium than upon the carnation agar, differences which would ordinarily be regarded as clearly of specific rank.

Alternaria Brassicae (Berk.) Sacc., from collard

This fungus made hyaline mycelium in CBA and CBA+sodium asparaginate; black mycelium in CBA+sodium asparaginate+glucose and in CBA+sodium asparaginate+starch, starch producing by far the most pronounced effect.

Digestion of the starch grains, somewhat in advance of the tips of the oncoming fungous threads, produced a clear zone surrounding each colony in the starch-bearing plates.

Ascochyta Chrysanthemi Stevens

This fungus was grown in the usual media with no significant effects, except that the fungus did not digest the starch grains afforded in the medium.

A deposit of great thickness around mycelial threads was made in the case of certain media and not in others, as has already been noted.[10]

In some instances culture at a high temperature occasioned this same reponse.

[10] Bot. Gazette 44:241. 1907.

SUMMARY OF CHEMICAL RELATIONS NOTED

The most striking response to chemicals is in color, which so far as observed was invariably heightened by the presence of chemicals bearing carbon in available form, the form of available carbon varying for different fungi. Some fungi, possessing ability to digest starch, can utilize this as a source, while to others the carbon of starch is inaccessible. Special unknown chemicals in apple add vivid colors to fungi otherwise hyaline. Some chemicals also promote or inhibit spore formation. Some inhibit or promote growth of setae and some even alter the size, color, and septation of spores. MILBURN,[5] working under KLEBS, has also noted pronounced effects of chemicals upon the color of fungi. The difference in color effects produced by different fungi under the same conditions, and with the same fungus under different conditions, is also noted by BESSEY.[9] No correlation is noted between rapidity of lineal growth and nutritive value of the medium. In many instances most rapid lineal growth occurred in what was surely the poorest medium. Very poor media suffice in many cases also for spore formation, while rich media often result in cessation of spore formation.

Colletotrichum Lindemuthianum, sometimes with setae, often without, has long been of questionable generic position. The same is true of several other species of this genus. *Alternaria Brassicae* and *Macrosporium Brassicae* agree closely except as to presence or absence of catenulate spores.[11] Variation of this kind is probably due to variation in chemical composition of the supporting medium, e. g., change in sugar content as ripening proceeds, acting in such way as to give the fungus the appearance of belonging to one genus when upon the green sugar-tree fruit, to another genus as the starch gives place to sugar as the fruit ripens.

IV. Light relation

The absence of material effect of light upon lineal growth with these species of fungi is shown in Table I.

Ascochyta Chrysanthemi Stevens.—The growth is more floccose in darkness.

Phyllosticta sp.—This fungus forms its pycnidia in beautiful con-

[11] *A. Brassicae* "hyphis brevibus conidiis 60–80 × 14–18 μ, 6–8 septato-muralibus." *M. Brassicae* "hyphis obsoletis conidiis 50–60 × 12–14 μ, 5–11 septatis."

centric rings when in open room, i.e., alternate light and darkness, but in continuous darkness they were irregularly scattered. Culture no. 35 made concentric rings when in the light, and failed to do so

TABLE I

Relation of light to growth

Figures express growth in millimeters. The cultures marked "alternate" were kept several days in light and several days in dark; *L* light; *D* dark. Inoculated Dec. 8, 1908.

LIGHT CONDITION		DECEMBER									
		9	10	11	12	13	14	15	16	17	18	19
Macrosporium Brassicae	In light	germ	1		6	9	13	16	17	23	26	28
	Alternate light & dark	*L*	*L*	*L*		*L*	*D*	*D*	*D*	*L*	*L*	*L*
		germ	1		6	10	12	15	17	23	26	28
	In dark	germ	1		6	9	11	15	17	21	29	29
Phyllosticta sp.	In light	0	gr.		4	7	10	13	14	16	20	23
	Alternate light & dark	*L*	*L*	*L*	*L*	*L*	*D*	*D*	*D*	*L*	*L*	
		0	gr.		4	7	10	13	13	16	18	20
	In dark	0	gr.		4	6	7	10	13	16	19	20
Ascochyta Chrysanthemi	In light		4		12	15	17	25	26	33	39	41
	Alternate light & dark	*L*	*L*	*L*	*D*	*D*	*D*	*D*	*D*	*L*	*L*	*L*
		2	3		12	16	20	25	30	37	39	45
	In dark				12	14	18	22	25	31	37	37

when moved to darkness. Cultures kept in the open room lay down rudiments of pycnidia mainly during the night, and it is probable that light exerts enough inhibiting influence on pycnidial development to give a growth predominance during the day and a fructifying predominance during the night (HEDGECOCK, *l. c.*[4]).

Alternaria Brassicae (Berk.) Sacc.—With this fungus the end of each day's growth, evening, marks the edge of a zone. The zone thus marked is intensified during the succeeding twenty-four hours by color changes. While zones are formed to some extent in continued darkness, they are more pronounced in the room condition.

SUMMARY OF LIGHT RELATION

Light exerts little or no effect upon lineal growth with these fungi. It appears to exert an inhibiting influence on pycnidial development and in some instances is the cause of zonation in colonies.

V. Unknown factors

Ascochyta Chrysanthemi Stevens

This fungus frequently exhibited differences in character along different radii of the same colony, the conditions of medium, thickness of sowing, humidity, etc., being apparently identical.

Fig. 12 shows such a colony. Along the radius *aa*, at *b*, the colony bore pycnidia abundantly, and the mycelial progeny of this strain extending to the periphery of the colony was rich in pycnidia, while

Fig. 12.—*Ascochyta Chrysanthemi* Stevens, showing abundant pycnidia on radius *aa*, at the point *b*, and paucity of pycnidia elsewhere.

most other radii of the colony were sterile or nearly so. Transfers were made from the point *c* (sterile) and *d* (pycnidial) to fresh plates. The sterile mycelium produced a colony which was sterile through its early days. As it aged it formed a few large pale pycnidia. The fertile strain produced a fertile colony with very numerous, though

small, pycnidia. Transfers made again from these two strains resulted in a complete reversal of character, the fertile becoming sterile and the sterile becoming fertile. No explanation of this suggests itself.

When this fungus was plated from a suspension of spores, two types of colony developed, corresponding to the two strains mentioned

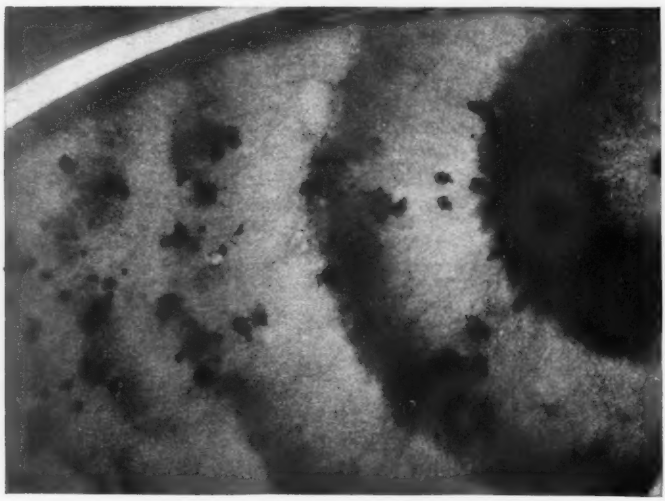

FIG. 13.—*Ascochyta Chrysanthemi* Stevens; portion of colony showing few pycnidia; cf. *fig. 14*.

above. The first "type of few pycnidia" developed a copious aerial mycelium of loose floccose nature, extended regularly in all directions, and was long devoid of pycnidia. When the pycnidia did form, they were few, large, and superficial (*fig. 13*). The second "type of many pycnidia" had little or no aerial mycelium, all the mycelium being either immersed or of strict growth; was roughly circular in colony, not regularly so as in first type; and small, irregular, mostly immersed pycnidia were formed in myriads throughout the colony (*fig. 14*). These two types of colony appeared on the same plates which were inoculated with spores from the same pycnidium. They therefore developed in the same nutrient condition, humidity, temperature, etc. Depth of planting was not the cause of these differences,

since flooding the plate with an extra tube of agar after the agar first plated had set, did not change the proportion of the two types. Nor did sowing in such way that the spores were at the bottom rather than at the top of the agar change results. There was a marked tendency of colonies of both types of the fungus to become more productive of large pycnidia where two different colonies approach each other, sug-

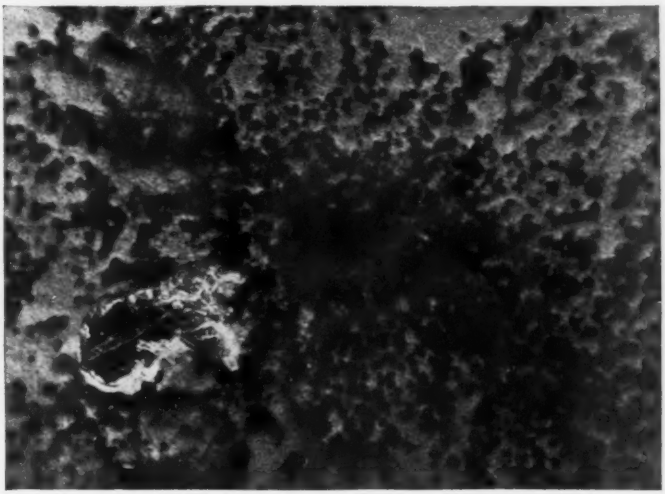

FIG. 14.—*Ascochyta Chrysanthemi* Stevens; portion of colony showing many pycnidia; cf. *fig. 13*.

gesting that there might be needed a cooperation of two diverse strains in order to form a pycnidium; that the strains of few pycnidia lacked the requisite individuals, and that the strains of many pycnidia had more than one individual to the colony. To test this, colonies were traced from the earliest development, resulting in clear evidence that in some instances a colony developed from a single spore was one with few pycnidia; in other instances a single spore produced a colony of many pycnidia.

CONIOTHYRIUM FUCKELII SACC., FROM APPLE

In one instance this fungus, which rarely fruited, made pycnidia in almost perfect circles near the margins of each colony on the plate (*fig. 15*).

These variations are inexplicable and remind one of the mysterious change from the ascigerous to the non-ascigerous condition so frequently met in life-history work with the imperfect fungi.

Variability in spore measurements

Since the beginning of mycology it has been customary to give spore measurements in specific description, probably originally with

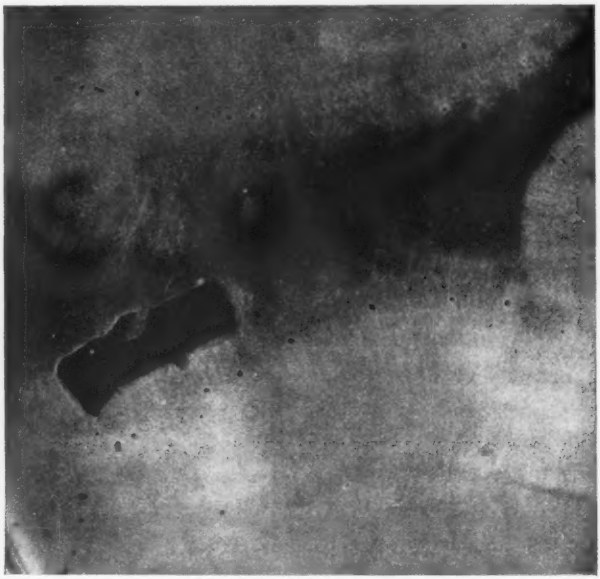

FIG. 15.—*Coniothyrium Fuckelii* Sacc.; portions of two colonies showing circles of pycnidia near margins.

the idea of giving some information as to the approximate size of the plant concerned rather than to give exact descriptive limitations. With the advance of time, great importance has come to be attached to spore measurements, greater perhaps than is warranted, and many species are now founded upon divergence in this one character—and often upon slight divergence.

To ascertain the variability in spore measurement under constant conditions and its variability as occasioned by changes in environment, studies with several species of fungi were undertaken.

The measurements were all made in water in which the spores had stood long enough to become fully turgid, taking only such spores as were completely ripe, as was shown by the fact that they were extruded from the pycnidium, ascus, or sporodochium naturally, without assistance. An eyepiece micrometer was used and the units here employed are usually one division of the eyepiece scale (equal to 3.7 μ), which constituted in most cases as small a unit as could be used to advantage. Spore measurements involving half the division were recorded as with the next lower integer unless otherwise designated. To avoid any possibility of unconscious selection, the spore lying closest to contact with the end of the micrometer scale at the completion of a measurement was taken for the next measurement. In the polygons each small square (one 256th of a square inch) represents one spore.

We wish to acknowledge our indebtedness to Dr. G. H. SHULL, who has kindly read this portion of the manuscript, for calculating the constants, and to Mr. B. B. HIGGINS, by whom most of the measurements were made and upon whose very accurate and painstaking work the value of the measurements depends.

ASCOCHYTA CHRYSANTHEMI STEVENS

A. *Spores from the large pycnidium type* (see p. 18)

Pycnidium no. 1. A large pycnidium produced in a colony which had very few pycnidia.

$M = 4.9645 \pm 0.0393$
$\sigma = 0.9787 \pm 0.0278$
C. V. $= 19.714 \pm 0.581$
$n = 284$

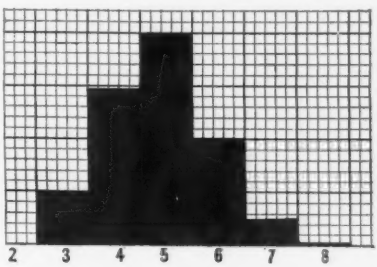

FIG. 16. — *Ascochyta Chrysanthemi* Stevens. Polygon of spores from pycnidium no. 1, large type. 3 should cover 20 squares instead of 25.

Pycnidium no. 2. Large type.

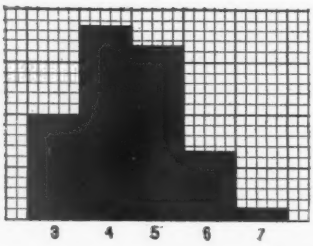

FIG. 17.—*Ascochyta Chrysanthemi* Stevens. Polygon of spores from pycnidium no. 2, large type.

$M = 4.4318 \pm 0.0398$
$\sigma = 0.9589 \pm 0.0281$
C. V. $= 21.638 \pm 0.650$
$n = 254$

Pycnidium no. 3. From a plate bearing one large colony. The whole colony was characteristically one of few pycnidia, which were of large type and light color. The spores were obtained without any possibility of the pycnidium being torn; that is, they were normally ripe spores.

$M = 3.3848 \pm 0.0245$
$\sigma = 0.6714 \pm 0.0173$
C. V. $= 19.836 \pm 0.531$
$n = 343$

It is seen that these three separate pycnidia of the same type gave modes of 4.9645 ± 0.0393, 4.4318 ± 0.0398, and 3.3848 ± 0.0245; or, expressed in terms of the systematist, that in the three pycnidia the spores measured 11.1–29.6 μ, mostly 18.5 μ; 11.1–25.9 μ, mostly 14.8 μ; 7.4–22.2 μ, mostly 11.1 μ; showing that measurements from one pycnidium alone are not sufficient for reliable characterization.

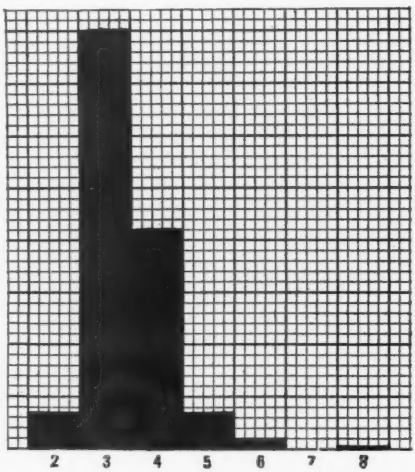

FIG. 18.—*Ascochyta Chrysanthemi* Stevens. Polygon of spores from pycnidium no. 3, large type.

B. *Spores from small pycnidium type* (see *fig. 14*)

Pycnidium no. 4. Small type.

M= 3.6011±0.0363
σ= 0.7183±0.0256
C. V.=19.947 ±0.740
n=178

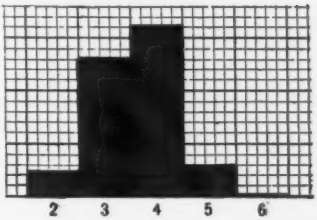

FIG. 19.—*Ascochyta Chrysanthemi* Stevens. Polygon of spores from pycnidium no. 4, small type.

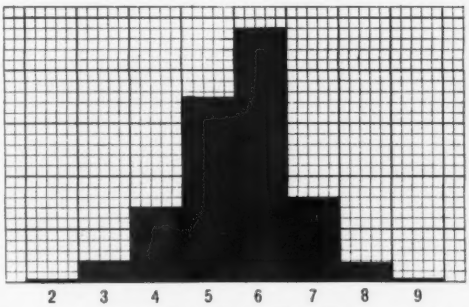

FIG. 20.—*Ascochyta Chrysanthemi* Stevens. Polygon of spores from pycnidium no. 5, small type.

Pycnidium no. 5. Spores taken from small pycnidia from colony shown in *fig. 14*.

M= 5.5850±0.0414
σ= 1.0737±0.0293
C. V.=19.225 ±0.543
n=306

Pycnidium no. 6. A very small pycnidial type.

M= 5.3629±0.0544
σ= 1.2711±0.0385
C. V.=23.702 ±0.756
n=248

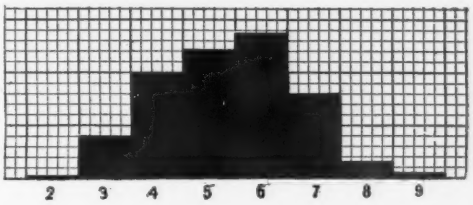

FIG. 21.—*Ascochyta Chrysanthemi* Stevens. Polygon of spores from pycnidium no. 6.

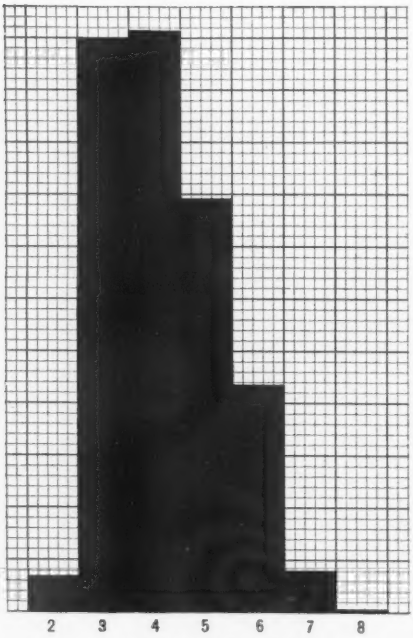

FIG. 22.—*Ascochyta Chrysanthemi* Stevens. Polygon of spores of large pycnidia.

Collecting the data from the large pycnidium type in one polygon, and similarly with the small pycnidium type we have:

$M = 4.1935 \pm 0.0247$
$\sigma = 1.0902 \pm 0.0174$
C. V. $= 25.998 \pm 0.443$
$n = 889$

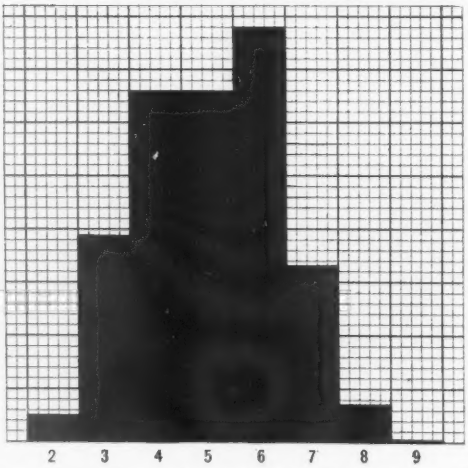

FIG. 23.—*Ascochyta Chrysanthemi* Stevens. Polygon of spores of small pycnidia.

$M = 5.0379 \pm 0.0335$
$\sigma = 1.3492 \pm 0.0237$
C. V. $= 26.781 \pm 0.503$
$n = 738$

It is seen that there is a tendency throughout for the smaller pycnidia to produce larger spores than are produced by the large pycnidia.

C. *Measurements of spores from different media*

Pure agar. The pycnidia on this plate were very scant, although they were normal in appearance and size.

$M = 2.6241 \pm 0.0313$
$\sigma = 0.5354 \pm 0.0221$
C. V. $= 20.402 \pm 0.878$
$n = 135$

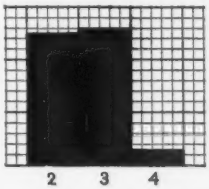

FIG. 24.—*Ascochyta Chrysanthemi* Stevens. Polygon of spores from pure agar.

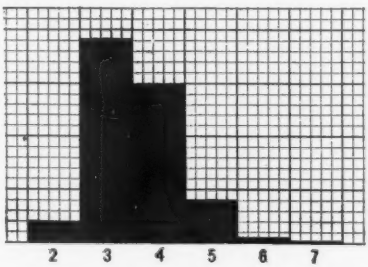

FIG. 25.—*Ascochyta Chrysanthemi* Stevens. Polygon of spores from CBA + 0.25 per cent sodium asparaginate.

CBA + 0.25 per cent. sodium asparaginate.

$M = 3.5637 \pm 0.0358$
$\sigma = 0.7579 \pm 0.0253$
C. V. $= 21.267 \pm 0.725$
$n = 204$

CBA + sodium asparaginate + starch.

$M = 5.4267 \pm 0.0355$
$\sigma = 0.7896 \pm 0.0251$
C. V. $= 14.551 \pm 0.459$
$n = 225$

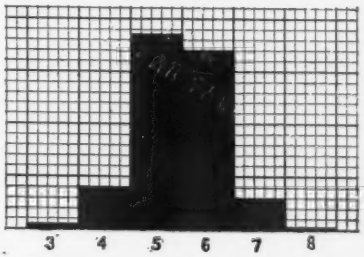

FIG. 26.—*Ascochyta Chrysanthemi* Stevens. Polygon of spores from CBA + sodium asparaginate + starch.

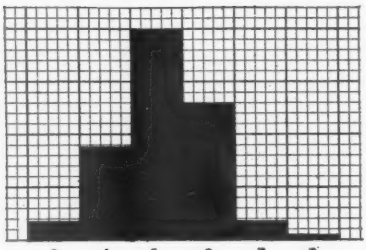

FIG. 27.—*Ascochyta Chrysanthemi* Stevens. Polygon of spores from CBA+sodium asparaginate+glucose.

CBA+sodium asparaginate+1 per cent. glucose. This was a remarkable colony with spores distinctly smoky or olivaceous.

$M = 5.1422 \pm 0.0408$
$\sigma = 0.9214 \pm 0.0289$
C. V. $= 17.919 \pm 0.579$
$n = 232$

Plated thickly in 4 per cent. pea agar.

$M = 4.3246 \pm 0.0392$
$\sigma = 1.0138 \pm 0.0277$
C. V. $= 23.442 \pm 0.674$
$n = 350$

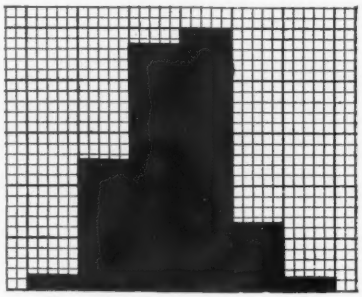

FIG. 28.—*Ascochyta Chrysanthemi* Stevens. Polygon of spores from 4 per cent. pea agar.

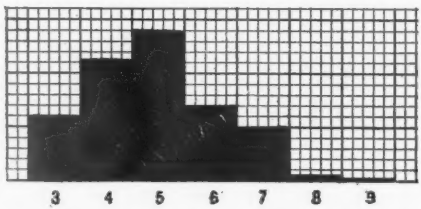

FIG. 29.—*Ascochyta Chrysanthemi* Stevens. Polygon of spores from cow pea agar.

Cow pea agar.
$M = 4.8657 \pm 0.0545$
$\sigma = 1.1885 \pm 0.0386$
C. V. $= 24.427 \pm 0.839$
$n = 214$

It is seen that on these different media the mode varies materially, being low on pure agar, higher on CBA+sodium asparaginate, and still higher when glucose or starch is added. The mode is high also in natural media, such as pea agar and cow pea agar.

In the terms of the systematist, spores from pure agar measured 7.4–14.8 μ, mostly 11.1 μ; those from CBA+sodium asparaginate 7.4–25.9 μ, mostly 12.9 μ.

SEPTORIA LYCOPERSICI SPEG. OF TOMATO

Grown on apple agar.

M = 21.507 ± 0.190
σ = 4.686 ± 0.135
C. V. = 21.787 ± 0.655
n = 278

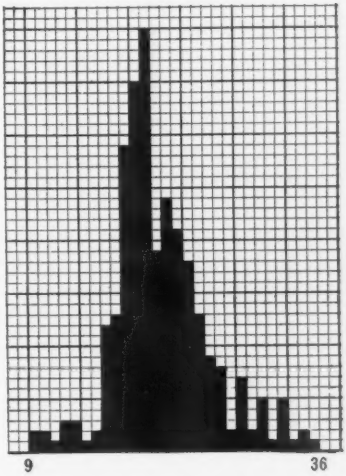

FIG. 30.—*Septoria Lycopersici* Speg. Polygon of spores on apple apar.

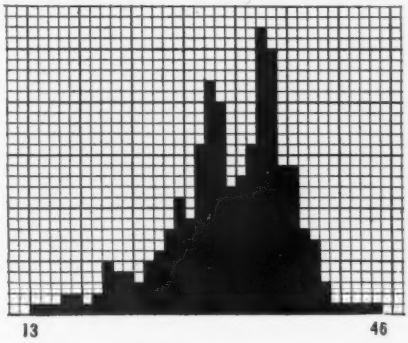

FIG. 31.—*Septoria Lycopersici* Speg. Polgyon of spores on pure agar.

Grown on pure agar.

M = 31.675 ± 0.242
σ = 5.879 ± 0.171
C. V. = 18.560 ± 0.559
n = 279

Although the number of spores measured in the two last instances is not large, the fact of a tendency to larger spores on the poorer medium, apple agar, is evident. The spores measured 33.6–133.2 μ, mostly 81.4 μ; those on pure agar 48.1–181.3 μ, mostly 133.2 μ.

Ascospores of Sclerotinia Libertiana Fuckel

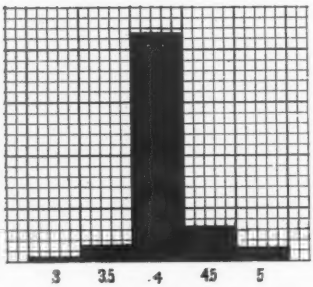

FIG. 32.—*Sclerotinia Libertiana* Fckl. Polygon of ascospores from middle-aged disk.

Spores were discharged spontaneously from the disk upon the cover glass, the disk being of middle age.

$M = 4.0880 \pm 0.0166$
$\sigma = 0.2930 \pm 0.0117$
C. V. $= 7.168 \pm 0.290$
$n = 142$

Spores were secured as in the last instance, but from very young disks.

$M = 4.0393 \pm 0.0214$
$\sigma = 0.3743 \pm 0.0151$
C. V. $= 9.267 \pm 0.380$
$n = 165$

No material difference in the size of the spores here appeared with the change in age of the disks.

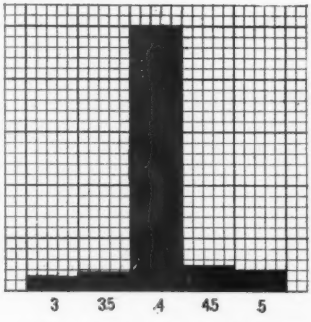

FIG. 33.—*Sclerotinia Libertiana* Fckl. Polygon of spores from young disk.

Diplodia macrospora Earle

Spores of this species, isolated from corn, were grown upon pea agar.

$M = 24.362 \pm 0.176$
$\sigma = 3.179 \pm 0.124$
C. V. $= 13.050 \pm 0.519$
$n = 149$

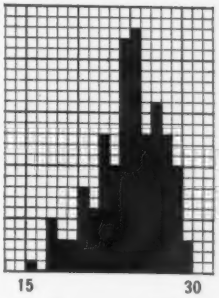

Fig. 34. — *Diplodia macrospora* Earle. Polygon of spores isolated from corn and grown upon pea agar; measurements showing length.

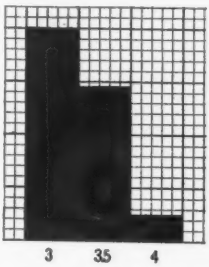

Fig. 35.—*Diplodia macrospora* Earle. Polygon of spores isolated from corn and grown upon pea agar; measurements showing thickness.

$M = 3.2595 \pm 0.136$
$\sigma = 0.2727 \pm 0.0096$
C. V. $= 8.367 \pm 0.297$
$n = 183$

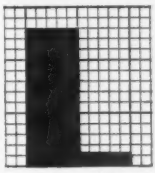

Fig. 36.—*Volutella fructi* S. & H. Polygon of spores showing width.

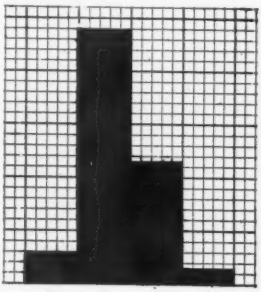

Fig. 37. — *Volutella fructi* S. & H. Polygon of spores showing length.

Volutella fructi S. & H.

$M = 8.27 \pm 0.0276$
$\sigma = 0.5778 \pm 0.0195$
C. V. $= 6.986 \pm 0.237$
$n = 200$

The last five polygons are without particular significance and serve only to show the variation encountered in these forms.

General considerations

The bearing of these facts upon mycological taxonomy is apparent. If a fungus can be easily changed as regards its essential descriptive characters by a change in substratum, density of infection, or other environmental factor, these characters are worthless for descriptive purposes, unless the conditions under which they develop be accurately known.

There are two fundamental benefits from description: (1) to enable recognition of a particular form; (2) to aid in classification. The first of these is a necessary preliminary to the second, and it is with mere recognition that we have in many instances yet to deal in mycology, particularly among the group *Fungi imperfecti*, with its enormous genera, such as Septoria, Phyllosticta, and Cercospora, with their thousands of so-called species. While life-history work and infection experiments will do much, accurate recognition of the form in hand is a necessary preliminary even to this.

To reach any satisfactory basis, many fungi must be studied in culture, under suitable standard conditions, much after the fashion that bacteria are now studied.

North Carolina Agric. Exper. Station and College
West Raleigh

THE DEVELOPMENT OF THE GAMETOPHYTES AND FERTILIZATION IN *JUNIPERUS COMMUNIS* AND *JUNIPERUS VIRGINIANA*

ALICE M. OTTLEY

(WITH PLATES I—IV)

INTRODUCTION AND METHODS

The present paper is based upon a study of *Juniperus communis* and of *Juniperus virginiana*. *J. communis* was worked out more in detail, and throughout the following description it is the species referred to unless otherwise stated. Since this study was begun, two papers, SLUDSKY (**22**) and NORÉN (**20**), based on a study of *J. communis*, have appeared. In the main NORÉN'S observations have been confirmed by the present study. He gave a very complete history of the literature relating to Juniperus and it will not be necessary to repeat it here.

The pistillate and staminate cones of *J. communis* were collected about one and a half miles southeast of Wellesley, Mass., those of *J. virginiana* from the campus of Wellesley College and near-by places. The collection of the material began the second week in March, 1905, and continued until the latter part of June of the same year. Fresh material was gathered once a week from March 13 through the first week in May; from May 8 until June 26 collections were made twice a week. The material was kept in water and put up approximately every other day. Pistillate cones of *J. communis* for 1903, 1904, and 1905, and of *J. virginiana* for 1905 were collected; the staminate cones were put up until the shedding of the pollen, which in 1905 was on May 9 for *J. virginiana* and May 11 for *J. communis*. The fixing agent used was Flemming's chromacetosmic solution and the stain gentian violet and orange G.

Besides the slides prepared from this material I have had the privilege of studying one hundred slides which were prepared by Miss FERGUSON in the spring of 1903. These were of great value in giving the approximate dates at which to look for certain desirable stages,

as well as in showing the variation in time of the occurrence of certain phenomena due to varying climatic conditions of different seasons. It is interesting to note that the different stages of development as worked out by NORÉN from material collected in Sweden were, in general, from three to four weeks later than corresponding stages in the material collected at Wellesley.

MALE GAMETOPHYTE

Both *J. communis* and *J. virginiana* are dioecious, occasionally monoecious. RENNER (**21**) reported the presence of hermaphrodite flowers in *J. communis*. I searched for similar flowers during the period of collection, but was unable to find any. The microsporangia were fully developed and the microspore mother cells were already present in *J. virginiana* on March 28, but in *J. communis* the microsporangia were not differentiated until April 13. The sporophylls are cyclic in arrangement and are disposed in whorls of three, with the microsporangia on the under side next to the axis of the cone (*fig. 1*). On April 25 the cells of the archesporial tissue were undergoing their last division before the formation of the microspore mother cells. Following this division, each microsporangium consists of a central mass of polygonal microspore mother cells; surrounding these is a single layer of tapetal cells, rich in protoplasm and containing large nuclei, and a wall of two layers of cells (*fig. 2*), as has been described by other writers. The cells of the outer or superficial layer of the wall are large and tabular. They contain considerable resin, which causes them to stain diffusely.

Very soon after the differentiation of the microspore mother cells the heterotypic division begins. LOPRIORE (**18**) reported that the microspore mother cells of *Araucaria Bidwillii* also undergo a very short period of rest before this division is entered upon. As soon as the walls are formed about each microspore, the mother wall breaks down, setting the spores free in the sporangium.

The microspores increased in size and were shed May 11. The mature pollen grains of Juniperus do not differ as to content from the microspores. In the spring of 1903 pollination took place in *J. virginiana* on April 22, but in the spring of 1905 not until May 9. There is, then, a variation, due to seasonal or climatic conditions, of

more than two weeks in the time at which the pollen may be shed. The microspore in *J. communis* and in *J. virginiana* undergoes no division in the anther, and so far as I have been able to determine no prothallial cells are ever formed in them. This agrees with the condition found in *J. communis* (BELAJEFF **2**, NORÉN **20**), in Biota and Cupressus (STRASBURGER **27**), and in *Taxus baccata*, *J. sphaerica*, and *J. chinensis* (COKER **6**). In Thuja (LAND **14**), Libocedrus and Chamaecyparis (LAWSON **17**), a division takes place while the pollen grains are still in the anther and gives rise to the tube and antheridial cells, but in these also no prothallial cells are ever formed.

The mature pollen grain has two walls, a deeply staining outer one and a faintly staining inner one (*fig. 3*). The outer wall of the pollen grains appears slightly roughened in many instances. When pollination takes place, the one-celled pollen grain comes to rest on the nucellar cap, the cells of which immediately lose their nuclei and become more or less disintegrated and collapsed, forming a depression in the top of the nucellus (*fig. 6;* NORÉN, *pl. 1, fig. 5*). Fifteen days after pollination the microspore divided to form the tube and the antheridial cells. The antheridial cell is the smaller of the two and remains always at one end of the pollen grain, while the tube cell is larger, possesses less dense cytoplasm, and its nucleus occupies the center of the pollen grain. Many starch grains are present at this time in the tube cell. The nucleus is large, with a loose chromatic network, and contains one nucleolus (*fig. 5*). As described by NORÉN (**20**), immediately after the division to form the antheridial and the tube cells, the pollen grain germinates, and the tube pushes its way down into the tissue of the nucellus, but by June 26 it has reached only a short distance. The tube nucleus migrates into the tube, but does not reach the end of it until the following spring; whereas in *J. virginiana* the tube nucleus passes at once into the tip of the tube (*fig. 8*), and fertilization takes place in the early summer of the same year.

Soon after germination in *J. communis*, the exine is shed in the pollen chamber and remains there, a dark-blue shell, as has been described for Taxodium by COKER (**5**). In many cases the pollen grain end of the tube is raised up above the nucellar tip into the pollen chamber, giving a peculiar appearance. This may be caused by the

germination of the pollen grain before it reaches the nucellus, or it may be that the pollen tube finds difficulty in piercing the tissue of the nucellar cap, and in the effort to do so the pollen grain end is pushed up into the pollen chamber. From the appearance of the pollen tube lying in a horizontal plane on the nucellar cap before the tip enters the nucellus, it seems quite probable that the latter explanation is the more suitable one.

The following spring the antheridial cell divides to form two nearly similar cells, the stalk and the generative cells. The division was not observed, but on May 8 the two cells had been formed and were seen in the pollen grain portion of the male gametophyte (*figs. 9, 10*). NORÉN gives no figure illustrating this stage and speaks only of a stalk nucleus. The two cells soon move down the tube. At first they are very similar in appearance, but in a short time the generative cell is easily distinguished by its larger nucleus, and by the fact that it retains its own cytoplasm; while that of the stalk cell is not distinguishable after passing into the tube, as in Thuja (LAND **14**) (*figs. 9–12*). Not until after the stalk nucleus has passed the generative cell does the nucleus of the latter appear larger than either the stalk or the tube nucleus (*fig. 12*). At this time the generative cell increases rapidly in size, and its nucleus becomes several times larger than either of the other two nuclei. The difference in size of these nuclei is more marked in *J. communis* (*fig. 13*) than in *J. virginiana* (*figs. 11, 12*). Neither in *J. communis* nor in *J. virginiana* is it possible, as stated above, to detect the cytoplasm of the stalk cell in the pollen tube. That the entire cell loses its connection with the wall of the pollen grain and starts into the tube is clearly shown in *fig. 10*. But very early in its downward course its cytoplasm fuses with the general cytoplasm of the tube and can no longer be distinguished from it.

The end of the tube with its cytoplasmic contents advances toward the female prothallium and spreads over the upper end of the archegonial complex (*fig. 27*). The generative cell takes its position in the center of the tube near the tip, and strands of protoplasm extend from it to the lateral walls of the pollen tube and below to the tip. The stalk and the tube nuclei, which are usually of the same size and can no longer be distinguished from each other, are side by side below

the generative cell. This corresponds with the condition at this time in Thuja as described by LAND (**14**). As noted by NORÉN, no starch appears in the pollen tube at this time. Previous to the division of the generative cell its cytoplasm becomes decidedly alveolar in appearance (*fig. 13*), suggesting the appearance of this cell in Zamia (WEBER **29**), Cycas (IKENO **9**), and Sequoia (LAWSON **15**). NORÉN does not speak of this appearance, but describes the cytoplasm as coarse grained and containing a large amount of finely divided starch which might easily escape observation. I was unable to find any signs of starch in this cell at any time in its history.

Just before fertilization the generative cell divides and forms two cells equal in size (*fig. 27*), as shown and described by NORÉN. This agrees with Biota (STRASBURGER **27**), Thuja (LAND **14**), Taxodium (COKER **5**), and Cryptomeria and Sequoia (LAWSON **15, 16**). When mature the two sperm cells in Juniperus are hemispherical in shape and lie with their flat sides face to face, but not in contact, as described by NORÉN, and in Thuja by LAND (**14**). The division of the generative cell occurs normally in Juniperus after the tube has reached the neck of the archegonium, but in one instance two similar nearly spherical cells which resembled generative cells appeared in the pollen tube when it was about half-way through the nucellus.

It would seem that the two sperm cells may both be capable of functioning, as LAND (**14**) thinks is the case in Thuja. They are equal in size, the archegonia are borne in complexes, and the tip of the pollen tube is pressed against the neck cells of several archegonia, thus making it possible for the sperm cells from one tube to enter different archegonia. Two or three pollen tubes may reach the same archegonial complex, and there is very little branching of the tubes in their way through the nucellus.

FEMALE GAMETOPHYTE

On March 28 the ovuliferous cones had appeared, but there were no indications of ovules. The first stages in their development were observed May 1. There are, as a rule, three ovules borne in the same horizontal plane at the apex of the cone. The integument arises as a little swelling at the base of the nucellus, and by May 8 it had passed beyond the top of the nucellus. But one integument is present, and

it is free to the base of the nucellus (*fig. 14;* NORÉN, *pl. 1, fig. 5*). The arms of the integument are composed of three to five layers of cells. The micropyle is wide and deep, and no depressed pollen chamber is present until after pollination. The nucellar cap is composed of large clear cells, which in the upper layer project up, thus giving a jagged or irregular outline to the top of the cap. The cells beneath these are smaller, more nearly isodiametric, are arranged concentrically, and contain large darkly staining nuclei (*fig. 14*). NORÉN does not find this concentric arrangement until after pollination.

At the time of pollination, a drop of clear liquid resembling a crystal bead is deposited on the top of each of the three ovules. It is probable that the pollen falls on this drop and is drawn down into the micropyle by the drying of the liquid, as has been described for other gymnosperms. The closing of the micropyle is brought about by the rapid elongation of the inner row of cells of the arms of the integument. Occasionally the two arms meet in a straight line (*fig. 15*), as in Pinus (FERGUSON **7**). More often, however, the arms dovetail together (*fig. 16*), also figured by NORÉN. By this method the micropyle is even more securely closed. Following the elongation of the cells cross-walls are laid down, cutting the lengthened cells into smaller ones. COKER (**5**) describes a similar elongation of the inner row of cells in Taxodium, while Miss FERGUSON (**7**) finds it in the middle row of cells in Pinus, and LAWSON (**16**) states that in *Cryptomeria japonica* the subepidermal and the epidermal rows both elongate. NORÉN reports that the closing of the micropyle in *J. communis* has recently been described by KUBART (**13**), but I have not seen this paper.

Soon, in the lower part of the nucellus, several faintly staining cells appear, the so-called spongy tissue of STRASBURGER. It is one of these cells that, in the following spring, is differentiated into the macrospore mother cell. It is very probable that it was the presence of this spongy tissue which led HOFMEISTER (**8**) to the opinion that the macrospore mother cell developed in early summer. NORÉN says that usually the macrospore mother cell could be distinguished by the beginning of July, but that occasionally two or four cells enlarge, and then it is impossible to tell which is the macrospore mother cell until the follow-

ing spring. In my material, the macrospore mother cell in *J. communis* was never differentiated until the spring following pollination.

Soon after pollination, May 11 for *J. communis*, the ovules cease to grow and remain practically the same size until the following spring (*figs. 15, 16*). In *J. virginiana*, however, the ovules continue to grow, the macrospore mother cell is differentiated, the female gametophyte is formed, and fertilization takes place in the latter part of June or the first of July of the same year in which the ovules were pollinated. SLUDSKY (**22**) described fertilization in *J. communis* as taking place in the same year as pollination. Both NORÉN's studies and the present investigation show that over a year elapses between pollination and fertilization in *J. communis*. It seems highly improbable that SLUDSKY could make a mistake in the age of the cones with which he was working, as suggested by CHAMBERLAIN (**3**) in a recent review in the BOTANICAL GAZETTE. Since the present study shows conclusively that the time elapsing between pollination and fertilization in different species of Juniperus may vary by nearly a whole year it seems far more probable that SLUDSKY was working with some other species than *J. communis*, and that in the species with which he worked fertilization does take place in the summer following pollination, as is the case in *J. virginiana*.

In *J. communis* growth began again in the early part of April. The macrospore mother cell appeared April 14 in the basal portion of the nucellus, and three days later the cell divided. In the prophase of the first division the cytoplasm is vacuolate except at one point, a short distance below the nucleus, where it is dense and stains more deeply (*fig. 18*), as noted by NORÉN. A similar densely staining mass of cytoplasm is present in all stages of division in the macrospore mother cell. No connection between this body and the division figures could be traced. COKER (**5, 6**) observed a similar condensation in Taxodium and in Thuja, but was unable to determine its significance. The presence of synapsis, the character of the spirem after synapsis, and the shape of the chromosomes indicate that this is a heterotypic division. In one slide studied there seemed to be evidence of a four-celled axial row, but from the material examined it was impossible to determine definitely whether the axial row consists of three or four cells. NORÉN states that there are three cells.

The basal cell of the axial row develops into the embryo sac. *Fig. 22* shows a two-celled embryo sac, with the disintegrating remains of the other cells of the axial row above it. Immediately after the first division of the macrospore nucleus, the two daughter nuclei take up a position at opposite poles of the embryo sac, and the cytoplasm becomes more vacuolate. The cells surrounding the developing prothallium are large, usually binucleate, and suggest a tapetum, as described for Taxodium by COKER (**5**). The nuclei of the prothallium divide simultaneously and form an ever-increasing ring of free cells (*fig. 23*). A layer of spongy tissue surrounds this ring and separates it from the other cells of the nucellus. By May 30 cell walls are laid down between the free nuclei, beginning at the periphery and extending toward the center. Contrary to SOKOLOWA'S (**23**) generalization for gymnosperms, and NORÉN'S observations for *J. communis*, cross-walls are formed before the central vacuole has entirely disappeared.

In the upper end of the prothallium a few cells do not divide by cross-walls, but remain long and narrow. These are the fundaments of the archegonia. By the latter part of May or first of June, the nuclei in these cells divide and give rise to the mother cell of the neck cells and to the central cell of the archegonium (*figs. 24, 25*). The central cell remains undivided until just before fertilization. Its nucleus is in the upper half of the archegonium, and below it is a large cylindrical vacuole. The cytoplasm stains faintly, and the nucleus contains several nucleoli. As a result of the division of the central cell, there arise the egg cell and the ventral canal nucleus. As observed by NORÉN (**20**) and SLUDSKY (**22**) no distinct ventral canal cell is ever formed. During the division the cytoplasm stains very deeply and presents a most peculiar appearance. Scattered throughout the entire cytoplasm are many bodies with deeply staining centers which are the so-called protein vacuoles. Three centers of radiations are present in the cytoplasm at this time, two below the large vacuole and one above it. The radiations appear to have no connection with the division of the central cell, but they are never seen so clearly at any other time as during this mitosis. Somewhat similar radiations are described by COKER (**5**) for Taxodium. NORÉN (**19, 20**) and SLUDSKY (**22**) figure and describe them for Juniperus,

but cannot explain them. *Fig. 26* shows these radiations in an early prophase of the division of the central cell.

After the ventral canal nucleus is cut off, it moves to the micropylar end of the cytoplasm and usually disorganizes before the pollen tube bursts. *Fig. 28* shows an unusually large ventral canal nucleus. The egg nucleus increases in size and moves slowly toward the central vacuole, taking up a position just above it. It usually possesses a beautiful chromatin network and a large nucleolus or several smaller nucleoli. At this time both the radiations and the protein vacuoles disappear, and many darkly staining specks appear in the egg cytoplasm (*fig. 27*). Contrary to what I have observed and SLUDSKY (**22**) has reported, NORÉN (**20**) says that these centers of radiations, so noticeable at the time of the division of the central cell, increase in size during the maturation of the egg. There is no evidence whatsoever of this in the material which formed the basis of the present study.

The archegonia form a complex which is surrounded by a layer of sheath cells. These are small and filled with deeply staining protoplasm. HOFMEISTER (**8**) says that Juniperus frequently has archegonia in abnormal positions and NORÉN has made the same observation. The only case of archegonia in abnormal positions that was observed, is shown in *fig. 36*. Here the archegonium is outside of the layer of sheath cells, but in other respects it appears normal.

FERTILIZATION

Fertilization follows directly upon the division of the generative cell and the maturation of the egg cell. In the summer of 1905 fertilization in *J. communis* occurred on June 17, 20, and 21. In ovules put up on the same day were found divisions of the central cell to form the egg cell and ventral canal nucleus, undivided generative cells, sperm cells, fertilization, and proembryos. This would indicate that these divisions take place very rapidly. A mass of densely staining, coarse-grained cytoplasm accompanies the sperm nucleus on its entrance into the egg. Whether the other contents of the tube enter the archegonium was not clearly determined; in one preparation there were densely staining bodies in the upper part of the archegonium, which might be the disorganized remains of the

other nuclei. NORÉN states that as a rule the two free nuclei do not enter the archegonium. The sperm cell loses its cytoplasm and passes directly to the egg nucleus. When the two nuclei have come in contact, they appear of about the same density and each contains a nucleolus and several secondary nucleoli (*fig. 29*). The only apparent difference is in size, the sperm nucleus being somewhat smaller. In one instance they were almost equal in size, and a dense mass of cytoplasm almost completely surrounded them.

This densely staining mass is doubtless the cytoplasm of the sperm cell (*fig. 30*). SLUDSKY (**22**) describes the nucleus of the functional sperm cell as escaping from its cytoplasm and fusing with the egg nucleus, while the rest of the sperm cell forms a cap over the fusion nucleus. Whether the two sexual nuclei fuse and form one nucleus could not be determined with absolute certainty. In one preparation a nucleus was present a little below the middle of the archegonium, with a small vacuole above it and one below it. The nucleus is at rest, a chromatic network is present, and a large nucleolus (*fig. 31*). It seems very probable that this is a fusion nucleus on its way to the bottom of the archegonium, as this is not the position which the egg nucleus ordinarily has before fertilization, and no other nucleus was present in this archegonium.

SLUDSKY (**22**) observed a large vacuole in the upper part of the archegonium after fertilization. He thinks this originates by the flowing together of the many small vacuoles, which he believes enter the archegonium from the pollen tube. It seems to me, however, that this vacuole is but the remains of the large vacuole present before fertilization. NORÉN (**19**) finds that the large central vacuole of the egg often disappears before the conjugation of the sexual nuclei.

In one case there occurred what appeared to be the fusion of the ventral canal nucleus with the second sperm nucleus. Two nuclei are present in the chalazal end of this archegonium. These are unquestionably the first two cells of the proembryo. Thus the fusing nuclei in the micropylar end of the archegonium cannot be the egg and the sperm nucleus (*fig. 35*). LAND (**14**) has reported a similar instance in Thuja and considers it a case of the fertilization of both the ventral canal nucleus and of the egg nucleus in the same archegonium.

PROEMBRYO AND EMBRYO

I cannot confirm STRASBURGER's (**24**) observation that the fusion nucleus moves to the organic apex of the archegonium before it divides. *Fig. 32* shows two nuclei in the resting stage and surrounded with cytoplasm of netlike appearance, about half-way between the middle of the archegonium and its lower extremity. While the cells of the proembryo are undergoing division, the cytoplasm is alveolar and very similar to that in the generative cell just before fertilization, except that the network is slightly finer (*fig. 34*).

Following fertilization, the three sporophylls of the pistillate cone fuse over the three ovules and form a berry-like fruit. As a rule the mature fruit contains but one or two seeds, the other ovules or ovule having ceased to grow before reaching maturity.

PHYLOGENY

From this study of Juniperus, it will be seen that in many respects this genus seems to be of more modern origin than many of the other gymnosperms. The cyclic arrangement of leaves and sporophylls, the absence of prothallial cells in the mature pollen grain, the absence of a ventral canal cell, and the presence of two functional sperm cells over an archegonial complex lead to this conclusion. JEFFREY (**10, 11**), in his investigations on the woods of the different gymnosperms, says that the wood of Juniperus and other Cupresseae indicates that they belong to a family more modern than the Abieteae. And THOMSON (**28**), as a result of his study of the development of the megaspore coat and of the tapetum, concludes that "the Abieteae are the most ancient group of the Coniferales and the Taxeae the most recent, that the Taxoideae and Podocarpeae are complex, including both ancient and recent forms; and that the Cupresseae occupy an intermediate position in the phylogenetic series."

SUMMARY

The staminate cones consist of many sporophylls, each bearing microsporangia on the under side near the axis.

The pistillate cones contain three ovules, each subtended by a sporophyll.

The mature pollen grain contains but one cell, no prothallial cells being present.

The macrospore mother cell first appears in *J. communis* one year after pollination. The first mitosis taking place within it shows clearly the stages characteristic of heterotypic division.

The contents of the pollen grain divide into antheridial cell and tube cell soon after pollination.

In *J. communis* the antheridial cell remains in the pollen grain and does not divide until April of the next spring.

In *J. virginiana* the antheridial cell divides in the early summer of the same year in which pollination takes place, and fertilization occurs in the latter part of June or first of July.

The generative cell and the stalk cell migrate immediately into the tube.

The stalk nucleus passes the generative cell and lies near the tube nucleus.

The generative cell does not divide until after the pollen tube has reached the archegonia and just before fertilization.

Two similar sperm cells are formed, each hemispherical in shape.

The female prothallium develops, as in the other gymnosperms, by free cell formation in a hollow sphere of cytoplasm. After many nuclei are formed, cell walls are laid down between them. These cells grow toward the center, but before they meet, cross-walls are laid down.

The archegonia develop from superficial cells at the micropylar end of the prothallium. They are arranged in a group, and the entire complex is surrounded by a single layer of sheath cells.

During the same day that the generative cell divides, and presumably before its division, the central cell of the archegonium divides.

A ventral canal nucleus is formed and remains throughout its life free in the cytoplasm of the egg, that is, no true ventral canal cell is ever cut off. This nucleus remains at the tip of the egg and, as a rule, soon disintegrates.

After fertilization the first division occurs before the fusion nucleus has passed to the organic apex of the archegonium.

In conclusion I wish to express my sincere gratitude to Professor

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EXPLANATION OF PLATES I—IV

The figures were drawn with the aid of an Abbé camera lucida. The degree of magnification is indicated in the description of each figure. The following abbreviations are used in connection with the figures. Antheridial cell, *a;* archegonium, *arch;* archesporial tissue, *a. t;* central cell, *c;* central nucleus, *c. n;* cytoplasmic condensation, *c. c;* egg nucleus, *e. n;* generative cell, *g;* inner wall, *i. w;* integument, *i;* micropyle, *M;* microspore mother cell, *Mi. m. c;* microsporangium, *Mg;* microsporophyll, *Mp;* nucellar cap, *n. c;* neck cells, *nk;* nucellus, *nuc;* outer wall, *o. w;* pollen chamber, *p. c;* prothallium, *pro;* protein vacuole, *p. v;* starch, *s;* secondary nucleoli, *s. nu;* sperm cell, *sp;* sperm nucleus, *s. n;* spongy tissue, *s. t;* sheath cell, *sh. c;* stalk cell, *st. c;* stalk nucleus, *st. n;* tapetum, *t;* tube cell, *t. c;* tube nucleus, *t. n;* ventral canal nucleus, *v. c. n.*

PLATE I

FIG. 1.—Longitudinal section of staminate cone of *J. communis;* April 25, 1905. ×62.

FIG. 2.—Microsporangium of *J. communis*, showing microspore mother cells, tapetum, and wall; May 1, 1905. ×382.

FIG. 3.—Mature microspore of *J. communis*, just before pollination. ×1850.

FIG. 4.—Pollen grain of *J. communis*, from the nucellus of an ovule, in prophase of first division; May 26, 1905. ×1850.

FIG. 5.—A two-celled pollen grain of *J. virginiana*, two weeks after pollination. ×1850.

FIG. 6.—Nucellar cap of *J. virginiana*, showing disintegration of cells beneath the pollen grain. ×116.

FIG. 7.—Early stage in the piercing of the nucellar cap by the pollen tube of *J. communis;* June 3, 1905. ×884.

FIG. 8.—Young pollen tube of *J. virginiana;* June 1, 1905. ×382.

FIG. 9.—Upper part of the pollen tube of *J. communis*, showing the stalk cell and the generative cell; May 8, 1905. ×1850.

FIG. 10.—Pollen tube of *J. communis*, showing the tearing-away of the cytoplasm of the stalk cell from the wall of the old pollen grain; May 10, 1905. ×884.

FIG. 11.—Portion of pollen tube of *J. virginiana*, midway through the nucellus, showing the generative cell with the tube and the stalk nuclei just beneath it. ×1850.

PLATE II

FIG. 12.—Lower portion of an older pollen tube of *J. virginiana*, showing the two free nuclei below the generative cell. ×1850.

FIG. 13.—The generative cell of *J. communis*, just before division; June 9, 1903. ×884.

FIG. 14.—Longitudinal section of ovule of *J. communis*, showing nucellus and integument; spongy tissue not yet clearly differentiated; May 19, 1905. ×116.

FIG. 15.—Longitudinal section of ovule of *J. virginiana*, showing an occasional method of closing the micropyle. ×116.

FIG. 16.—Longitudinal section of ovule of *J. communis* in winter condition, showing usual method of closing of micropyle; March 28, 1905. ×116.

FIG. 17.—Macrospore mother cell of *J. communis;* April 14, 1905. ×704.

FIG. 18.—Macrospore mother cell of *J. communis*, in prophase of division with spongy tissue around it; April 17, 1905. ×704.

FIGS. 19–21.—Different stages in the division of the macrospore mother cell of *J. communis;* April 17, 1905. ×1850.

FIG. 22.—Two-celled embryo sac of *J. communis;* May 1, 1905. ×704.

PLATE III

FIG. 23.—Longitudinal section of the nucellus of *J. communis*, showing the hollow prothallium almost a year after pollination; May 5, 1905. ×188.

FIG. 24.—Prothallium of *J. communis*, almost closed at the center, with archegonia at the micropylar end; May 30, 1903. ×62.

FIG. 25.—Stages in the development of archegonia in the same archegonial complex of *J. communis;* May 30, 1903. ×704.

FIG. 26.—Longitudinal section of archegonium of *J. communis*, at the time of the division of the central cell; nucleus in prophase of division; large central vacuole and prominent radiations; June 20, 1905. ×704.

FIG. 27.—Longitudinal section of an archegonial complex of *J. communis*, with the tip of the pollen tube above it; June 20, 1905. ×382.

PLATE IV

FIG. 28.—Upper portion of archegonium of *J. communis* just before fertilization; June 20, 1905. ×1016.

FIGS. 29, 30.—Conjugation of sexual nuclei of *J. communis*, showing sheath of denser cytoplasm; June 20, 1905. ×1850, 884.

FIG. 31.—Fusion nucleus of *J. communis* between two vacuoles; June 20, 1905. ×884.

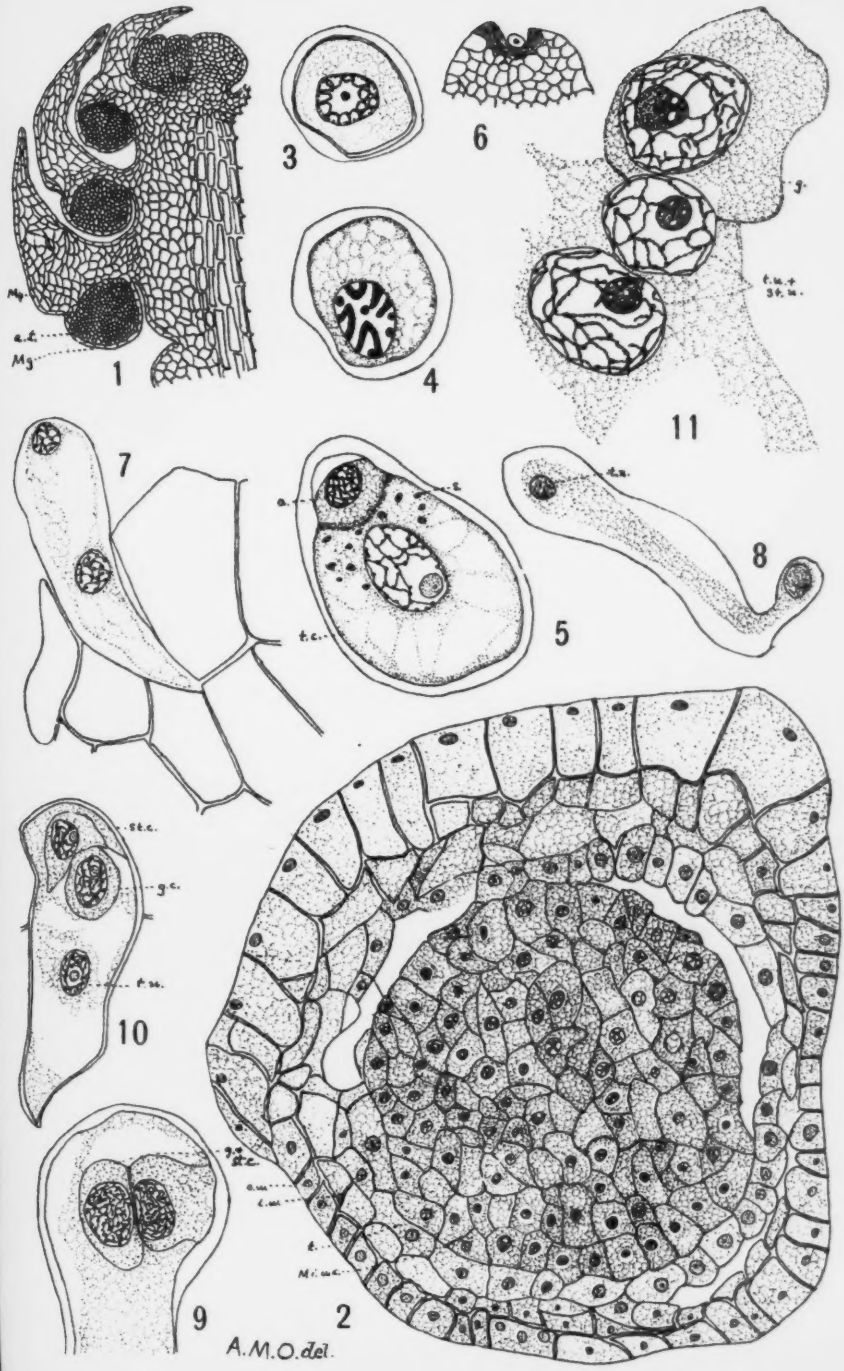
FIG. 32.—Two-celled proembryo of *J. communis*, surrounded by mass of nutritive substance; June 9, 1903. ×382.

FIG. 33.—Second division after fertilization at base of archegonium of *J. communis;* June 17, 1905. ×884.

FIG. 34.—Divisions to form the eight-celled proembryo of *J. communis;* June 20, 1905. ×884.

FIG. 35.—Probable fertilization of the ventral canal nucleus of *J. communis;* June 17, 1905. ×160.

FIG. 36.—Abnormal position of an archegonium of *J. communis*, just outside the complex; June 20, 1905. ×382.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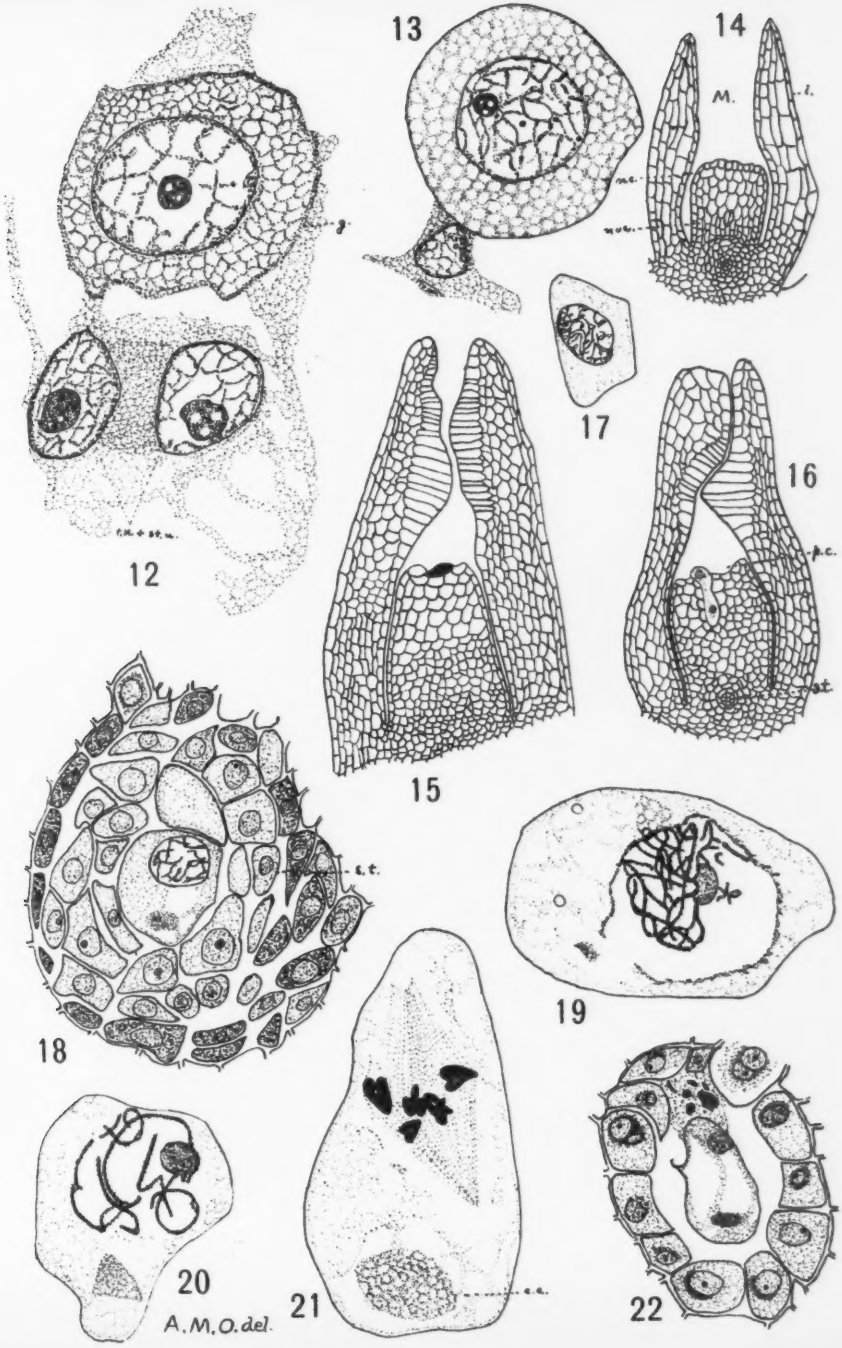
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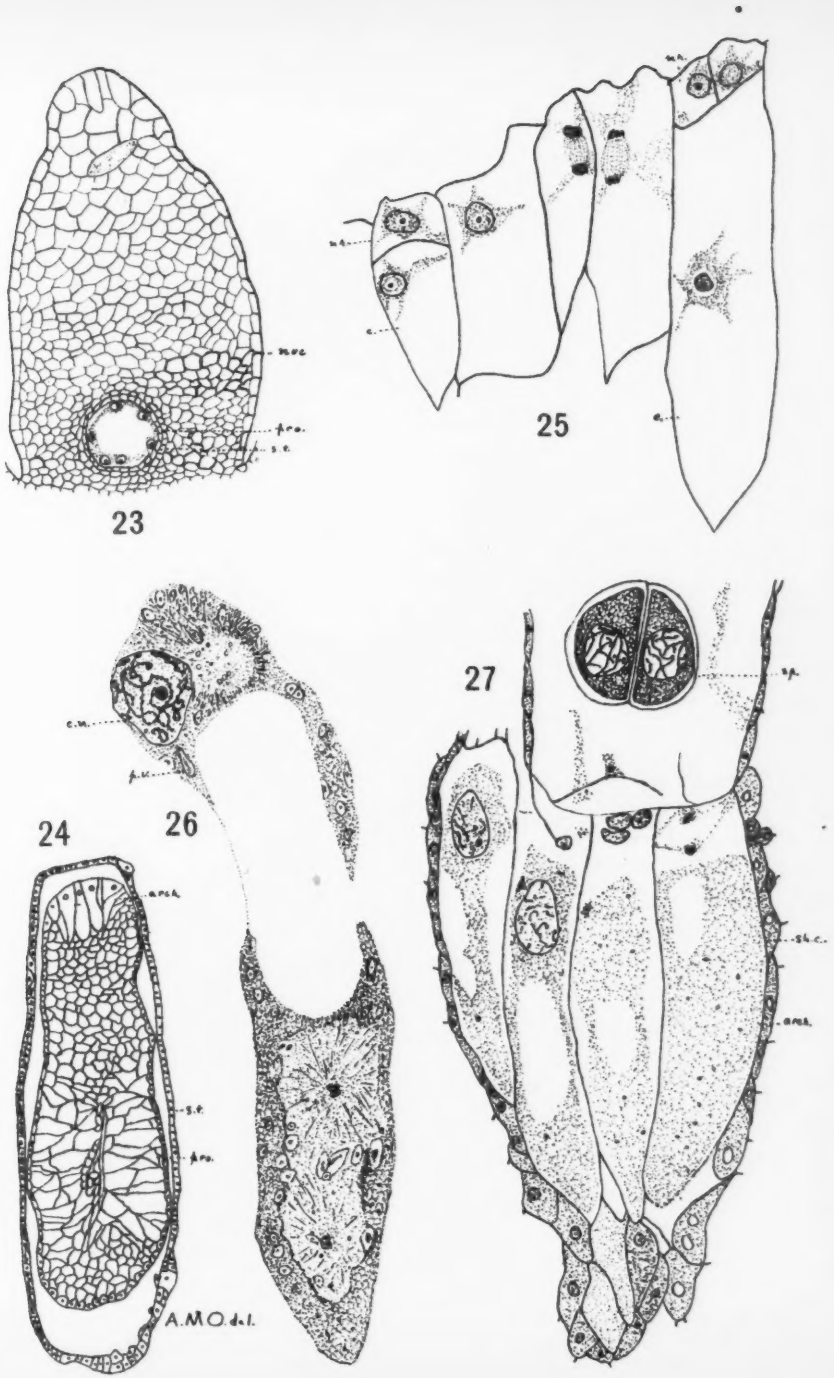
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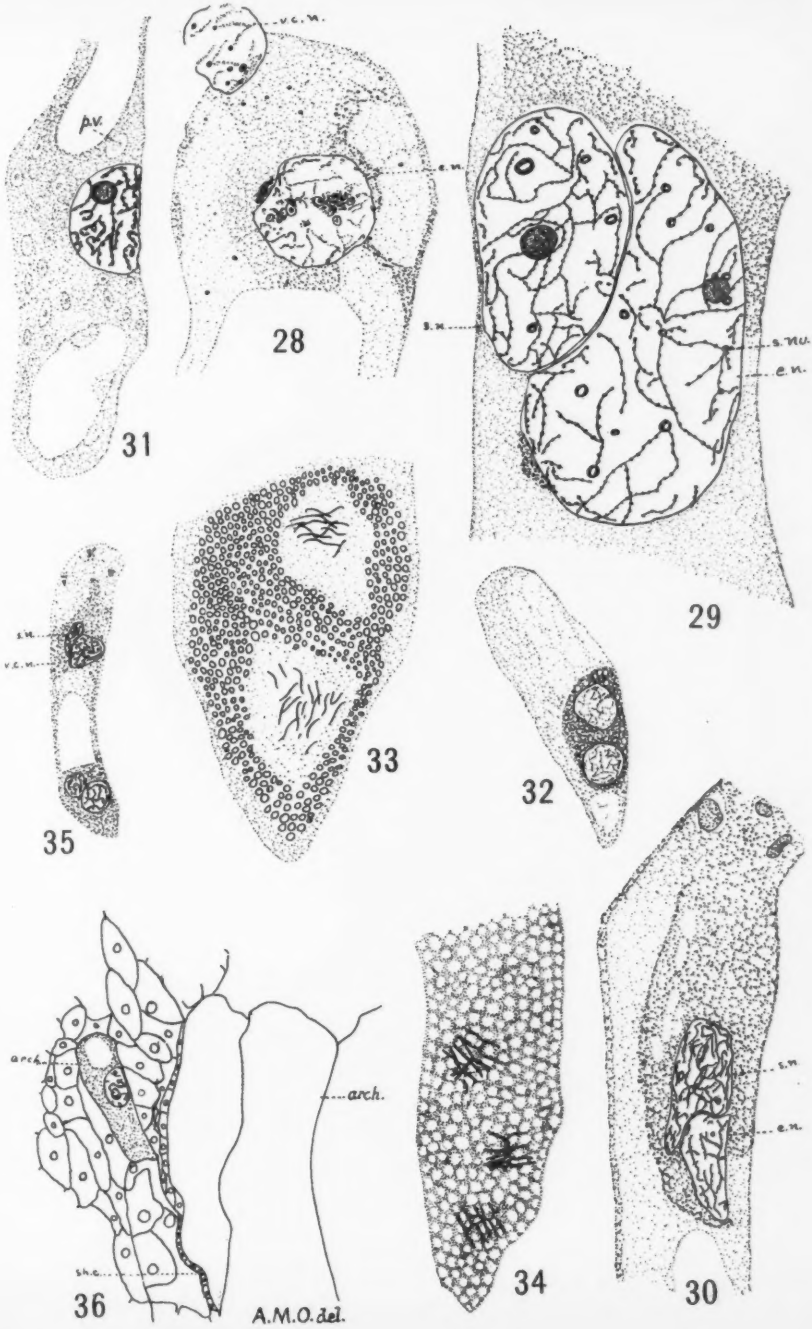
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THE STRUCTURE OF THE WOOD IN THE PINEAE[1]

IRVING W. BAILEY

(WITH PLATE V)

The Abietineae have been conveniently divided into the subfamilies Pineae and Abieteae.[2] The former are characterized by the presence of resin canals in the xylem, by their thinly integumented ovules, and by the non-deciduous character of the cone scales. The Abieteae differ in having resin canals absent from the woody tissues of the stem (except in the first annual ring of vigorous shoots of vigorous specimens of Abies), and by possessing usually a thick-coated ovule and deciduous cone scales. In both subfamilies resin canals may occur traumatically. These are easily differentiated from those normal to the stem by the fact that they occur in tangential rows of numerous canals, intercommunicating tangentially, and composed of generally heavily pitted epithelial cells. The Pineae comprise the genera Pinus, Picea, Larix, and Pseudotsuga. The Abieteae include Abies, Tsuga, Cedrus, and Pseudolarix. It will be the object of the present article to consider the structure of the woody cylinder in the former subfamily.

The four genera of the Pineae have been classified, by various authorities, according to the anatomical structure of the xylem as follows.

PINUS

The wood is characterized by the presence of numerous resin canals with thin-walled epithelium. This condition is constant except in the nut pines and foxtail pines of the southwestern United States, where thick-walled epithelial cells are interspersed among the usually thin-walled type. Further, Pinus is supposed to be characterized by the entire absence of wood-parenchyma, and according to GOTHAN of spiral thickenings of the tracheid walls of the secondary wood.[3]

[1] Contributions from the Phanerogamic Laboratories of Harvard University, No. 15.

[2] JEFFREY, The comparative anatomy and phylogeny of the Coniferales. Part 2. The Abietineae. Mem. Boston Soc. Nat. Hist. 6:21. 1905.

[3] GOTHAN, Zur Anatomie lebender und fossiler Gymnospermen-Hölzer. Abhandl. König. Preuss. Geol. Landesanstalt. Neue Folge, Heft 44, p. 99. Berlin. 1905.

The pines are divided into the hard pines and the soft pines. The former are characterized by possessing dentate or reticulate tracheids of the rays, and by having no tangential pits developed in the tracheids at the end of the year's growth. The soft pines, on the contrary, are supposed to possess marginal and interspersed tracheids of the rays with unsculptured walls, and to have well-developed tangential pits in the tracheids formed at the end of the year's growth. The majority of the hard pines and soft pines can easily be separated from the remaining genera of the Pineae by the character of the pits in the lateral walls of the parenchymatous cells of the rays. These pits are very large and often polygonal, and quite distinct from the small round pits of Picea, Larix, and Pseudotsuga. However, in the nut and foxtail pines above referred to, and in certain of the hard pines, we find a diminution in the size of the pits, which approaches the condition in the Picea type.

PICEA

Picea has a wood with thick-walled epithelial cells in the resin canals and tangential pits in the summer tracheids. The pits in the lateral walls of the ray cells are small and round. The wood-parenchyma is entirely absent. Spiral thickenings of the tracheids are also absent, according to PENHALLOW.[4] However, GOTHAN (*op. cit.* 98) and other European authorities note their presence in the summer wood alone.

LARIX

The wood resembles Picea as regards the thick-walled character of the resin canals, the presence of tangential pits in the summer tracheids, and the small size of the lateral pits of the ray cells; but possesses well-developed wood-parenchyma upon the outer surface of the summer wood. Spiral thickenings of the tracheids are present only in the summer wood.

PSEUDOTSUGA

The wood resembles Picea and Larix as regards thick-walled epithelium, tangential pits of the summer tracheids, and form and size of the pits of the ray cells. It also resembles Larix in having parenchyma well developed upon the outer surface of the summer wood. The wood, however, is supposed to be quite distinct in having well-

[4] PENHALLOW, North American Gymnosperms 195. Boston. 1907.

developed spiral thickenings in the spring as well as the summer tracheids. Further, according to MAYR,[5] spirals are also present in the ray tracheids of *Pseudotsuga macrocarpa* Mayr, but not in *P. Douglasii* Carr.

With this review of the generally accepted classification of the Pineae, let us turn to a careful consideration of the occurrence of each of the anatomical characters referred to above. In the first place as regards

WOOD-PARENCHYMA

As stated above, these cells are supposed to exist on the outer surface of the summer wood in Larix and Pseudotsuga, and to be entirely absent from Pinus and Picea. The presence of wood-parenchyma on the face of the summer wood in the xylem of a specimen of *Picea excelsa* Link in the Harvard Botanical Gardens led me to study this tree, believing that it was an unusual or freak specimen. The examination of sections from the root and stem showed the parenchyma well developed at the end of the year's growth (*figs. 1–3*), but in many cases the parenchymatous cells were rare or apparently absent from the stem. However, numerous sections cut from the same piece of wood always revealed one to several cells. It is difficult to see them in a transverse section, as they can be distinguished with certainty only when the simply pitted walls are visible. Obviously, to obtain this condition when the cells are rare is difficult. Likewise, in radial sections it is not easy to find them. If, however, tangential sections are cut in a slightly oblique manner, several layers of summer wood are visible in a single section. Many sections cut in series would then be more liable to reveal the presence of parenchymatous cells even when occurring infrequently. Cutting the sections in series avoids the possibility of confusing the parenchyma, for which I was searching, with that associated with resin canals or wound callus. However, the appearance of the latter as well as their location (not confined to the outer layer of the summer wood) is sufficient for their identification without these precautions.

I decided to use this method in the examination of other specimens of *Picea excelsa*, to see if wood-parenchyma were characteristic of the species. Upon examination it was found that the cells were present

[5] MAYR, Die Waldungen von Nordamerikas 424. *pl. 9.* München. 1890.

in *Picea excelsa* vars. *monstrosa*, *conica*, *elata*, *pendula*, and *pyramidalis*. Finding them characteristic of these varieties of the commonly planted *Picea excelsa*, it was decided to extend the studies to other species. Through the courtesy of Professor JACK, of the Arnold Arboretum, I was able to secure carefully identified green material of seventeen species of American, Asiatic, and European spruces. Thin serial sections of this material showed that the presence of wood-parenchyma upon the outer surface of the summer wood is a characteristic condition for Picea. Its occurrence, however, is extremely sporadic. In any given fragment of wood the cells may or may not appear, and while usually occurring very infrequently, may at any time appear in large numbers. These cells appeared more numerously in the European and Asiatic species, and in *Picea sitchensis* Carr. and *Picea Parryana* Sarg. of the American species. In the spruces from the northeastern United States they could be made out only with difficulty.

The extremely variable occurrence of wood-parenchyma is also characteristic of Larix and Pseudotsuga, for though usually occurring numerously upon the outer surface of the summer wood, in many specimens they may be very infrequent or nearly absent.

SEPTATE TRACHEIDS

In the three genera of the Pineae just mentioned septate tracheids occur with the parenchyma upon the outer surface of the year's growth. In Picea they are usually more numerous than the wood-parenchyma and occur where wood-parenchyma is not developed. In Larix and Pseudotsuga the parenchyma usually predominates. There is a clear gradation shown from tracheid to parenchyma in these genera. Frequently one may observe in the same section a septate tracheid, a tracheid partly septate and partly parenchymatous (*fig. 4*), and a series of resin cells, together having the form of a tracheid. In other words, the various steps by which tracheids have been modified to form parenchyma are clearly shown. In support of these statements it may be well to add that primitive woods were composed entirely of tracheids and medullary parenchyma, and that only in the higher gymnosperms do we see the development of wood-parenchyma, first upon the outer surface of the summer wood, and later throughout

the year's growth in plants which have lost, or are in the process of losing, their resin canals. In the Pineae, in which resin canals occur normally, the parenchyma is confined to the end of the year's growth, and less well developed in the older genera, which have more numerously developed resin canals. Thus Pinus, with its large supply of resin canals, shows only the first steps in the development of wood-parenchyma. Septate tracheids occur infrequently upon the outer surface of the summer wood, and only in one instance have I been able to observe what appeared to be parenchyma in the same location. In Picea, with less well-developed resin ducts, the wood-parenchyma becomes constant, while in Larix and Pseudotsuga it is usually strongly developed. In the Taxodineae and Cupressineae, with the nearly complete disappearance of resin canals, the wood-parenchyma is well developed throughout the year's growth, as well as at the end of the summer wood. The Abieteae are transitional between the two groups. It seems probable, as JEFFREY has suggested in his paper on the Abietineae (*op. cit.* 26), that with the reduction of foliage in the Abietineae and Cupressineae, the freely anastomosing system of canals, with its large supply of resinous secretions for sterilizing wounds, became too great a burden, and that the system of resin cells was gradually developed to take its place. It is not my object to enter here into all the various phases of the controversy as to the age of the Abietineae, but recent paleontological evidence proves the great geological age of Pinus. Further, Prepinus is a primitive abietineous type with centripetal wood, resembling certain of the Cordaites, and at the same time closely allied to the true pines of the middle Cretaceous.[6] A survey of all the paleontological evidence, as well as a study of the anatomy and morphology of the modern Coniferales, seems to show conclusively the greater age of the Abietineae.

SPIRAL THICKENINGS

Let us now turn to a consideration of the occurrence and distribution of tertiary thickenings of the tracheid walls in the Pineae.[7] As stated above, PENHALLOW considers spiral thickenings absent from

[6] JEFFREY, Structure of the leaf in Cretaceous pines. Annals of Botany **21**:207–220. *pls. 13, 14.* 1908.

[7] It should be kept clearly in mind that these spirals are tertiary thickenings, and are entirely distinct from the so-called "spiral striations" of the secondary walls of the tracheids.

Picea, while European authorities note their presence only in the summer wood. In the seventeen species of Picea which I examined, I found spirals well developed in the summer wood of the first few years' growth, usually from the first or second to the tenth year. In older woods they are very sporadic in their development, in certain regions appearing well developed, but usually showing at best only feebly. In wounded areas they showed a tendency to be strongly developed. In two species, *Picea sitchensis* Carr. and *Picea Maximowiczii* Regel, the spirals were very strongly developed in the spring as well as the summer wood (*fig. 6*). Furthermore, in both of these species, spiral thickenings were well developed in the marginal and interspersed tracheids of the rays (*fig. 5*). They occurred in the ray tracheids in both the summer and spring wood. In other species of Picea this condition could be made out in the tracheids of the rays of the summer wood. In other words, the ray tracheids appear to follow closely the wood tracheids. Where spirals are strongly developed in the latter elements, they will appear usually in the former.

In Larix the spirals were observed occurring in the first few years' growth, but not so well developed as in Picea. In the mature wood and in the ray tracheids, the spirals are likewise sporadic in their appearance, and may or may not be noticeably developed. Only four species were examined, *Larix americana* Michx., *L. europaea* DC., *L. occidentalis* Nutt., *L. dahurica* Turcz., and in none of these were spirals present in the spring wood; yet from the similarity to Picea and Pseudotsuga I should consider it extremely likely that they would be found, if a large amount of material were examined.

In Pseudotsuga spirals occur in both the summer and spring tracheids, yet they also are sporadic in their development, in certain specimens appearing well marked throughout, or in others nearly absent. MAYR notes the presence of spiral thickenings in the marginal tracheids of *Pseudotsuga macrocarpa* Mayr, but states (*loc. cit.*) that they are absent in *P. Douglasii* Carr. Sections from specimens of the Douglas fir from various sources show the spirals well developed in the marginal tracheids of certain specimens and less well developed in others.

In Pinus, as has been noted, GOTHAN asserts the absence of spirals, yet PENHALLOW (*op. cit.* 41) has described them as occurring in

Pinus taeda Linn., and I have myself observed them in *Pinus attenuata* Lemm. and several other species. Furthermore, spiral thickenings occur in the ray tracheids of *Pinus Balfouriana* A. Murr.; they are strongly developed in certain specimens and only feebly in others. *Pinus strobiformis* Engelm. and other pines from the southwestern United States show traces of their occurrence.

From the development of the spirals of the tracheids in the first year's growth and in areas of injury, it would appear that the spirals were an early development, yet the fact that they are not always present in the first and second annual rings, and are absent from the axis of the cone, would seem to show that the character cannot be primitive. It certainly would not be safe to assume that the presence of these spirals is an indication of close relationship with the Taxaceae, for spiral thickenings of the vessels in the dicotyledons are found in such widely separated families as the Betulaceae and Tiliaceae.

INSTABILITY OF DIAGNOSTIC CHARACTERS

From the preceding remarks on the development of wood-parenchyma and spiral thickenings, and the sporadic and uncertain character of their appearance, one realizes the difficulty in finding any definite basis upon which to separate Picea, Larix, and Pseudotsuga. As has been shown, one can no longer depend upon the presence or absence of wood-parenchyma and spirals to acomplish this end.

Let us now turn to consider the stability of the other elements of the wood. The size, form, and location of the resin canals vary so greatly in material from different sources that no rule can be formulated to cover every case. It is true that Picea approaches nearer to the condition found in the nut and foxtail pines than the other genera. Thus certain spruces have considerable thin-walled epithelium and tyloses, yet thin-walled epithelium occurs in Larix and Pseudotsuga. Further, the same variability is characteristic of the pitting of the rays and tracheids, and of the weight and color of the wood. We are thus forced to the conclusion that in order to distinguish the woods of Picea, Larix, and Pseudotsuga, a careful study must be made of all the anatomical and gross characters, and comparisons made with type sections. In other words, one must apply here the same methods in differentiating genera which one usually uses in distinguishing species.

As an illustration of the difficulty in distinguishing these woods let us consider a fossil from California recently described by GOTHAN.[8] He identifies the specimen as follows. The fact that the resin canals are typically non-pine-like, with thick-walled epithelium, shuts out Pinoxylon. The presence of wood-parenchyma and spirals in the spring wood shows its relation to Pseudotsuga. *Pseudotsuga macrocarpa* has ray tracheids with spirals, and in *P. Douglasii* they are absent. Thus the fossil, which he calls *Piceoxylon Pseudotsugae*, as it has no spirals in the ray tracheids, must be closely allied to the Douglas fir, if not a fossil specimen of it.

In the first place, as we have seen, *Pseudotsuga Douglasii* possesses spiral thickenings in the ray tracheids. This, according to the author's own line of reasoning, would exclude *P. Douglasii*. Further, let us consider the statements in regard to the presence of wood-parenchyma and spiral thickenings in the spring wood. As has been shown above, both these conditions occur in *Picea sitchensis*, a spruce from the Pacific coast. Can we be sure whether this fossil is more closely allied to Pseudotsuga, Picea, or even Larix? As an added reason for regarding the fossil allied to Pseudotsuga, the author states that the horizontal resin canals in the fusiform rays occur in an unsymmetrical manner. This same condition may be frequently observed in both Picea and Larix. One comes to the conclusion that the identification of woods and fossils of Picea, Larix, and Pseudotsuga is an extremely difficult undertaking.

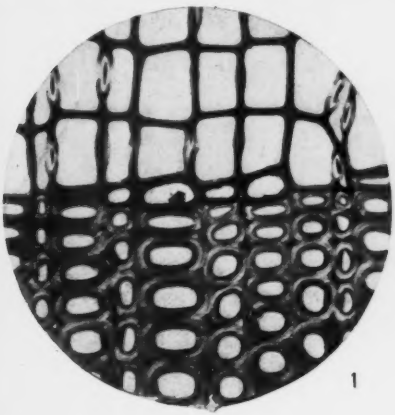
SUMMARY

1. Wood-parenchyma occurs on the outer surface of the summer wood of Picea. It is sporadic in its occurrence, and while usually appearing infrequently, may be strongly developed.

2. Wood-parenchyma may be very sparsely developed in Larix and Pseudotsuga.

3. Septate tracheids occur associated with the wood-parenchyma in these three genera, and show clearly the steps by which wood-parenchyma has been developed from tracheids.

[8] GOTHAN, *Piceoxylon Pseudotsugae* als fossiler Holz, *Pseudotsuga* sp. (aff. *Douglasii*) als rezenter Baum; in H. POTONIE, Abbildungen u. Beschreibungen Foss. Pflanzen, Lief 4. 1906.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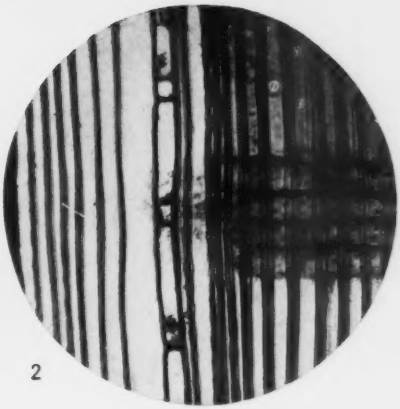
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BAILEY on WOOD OF PINEAE

4. Septate tracheids occur in Pinus, and wood-parenchyma very rarely.

5. Spiral thickenings of the tracheids occur in both the spring and summer wood in Picea and Pseudotsuga, and occur in the summer wood of Larix. These thickenings occur also in Pinus.

6. Spiral thickenings of the marginal and interspersed tracheids of the rays occur in Pinus, Picea, and Larix, as well as in Pseudotsuga.

7. The anatomical characters of the wood are so variable and so similar in Picea, Larix, and Pseudotsuga, that it is difficult to distinguish the extant or fossil woods of the genera.

8. Pinus appears to be quite distinct from the other living Pineae. Yet in the nut and foxtail pines, we see a condition resembling the condition in Picea, Larix, and Pseudotsuga. These pines have small rounded pits in the ray cells, have tangential pits like Picea, have thick-walled epithelium in the canals, and spiral thickenings in the ray tracheids.

9. Picea approaches nearer to the condition in Pinus by having more numerous thin-walled epithelial cells and tyloses, and less well-developed wood-parenchyma; yet Larix and Pseudotsuga also have thin-walled epithelial cells occasionally, and may have the wood-parenchyma poorly developed.

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EXPLANATION OF PLATE V

FIG. 1.—Transverse section of stem of *Picea excelsa*, showing four resin cells on the outer face of the summer wood. ×500.

FIG. 2.—Radial section of root of *Picea excelsa*, showing resin cells on the outer face of the summer wood. ×180.

FIG. 3.—Tangential section of root of *Picea excelsa*, showing resin cells. ×180.

FIG. 4.—Radial section of root of *Picea excelsa*, showing tracheid partly septate and border-pitted, and partly parenchymatous and simply pitted. ×180.

FIG. 5.—Radial section of stem of *Picea Maximowiczii*, showing spiral thickenings in the marginal tracheids. ×900.

FIG. 6.—Tangential section of stem of *Picea Maximowiczii*, showing spiral thickenings in both the spring and summer wood. ×180.

BRIEFER ARTICLES

NOTES ON THE EMBRYOLOGY OF THE NYMPHAEACEAE

(WITH PLATE VI)

Within the past few years the embryology of the Nymphaeaceae has attracted considerable attention, beginning with LYON's studies on Nelumbo,[1] followed by my own paper on *Castalia odorata* and *Nymphaea advena*[2] and by CONARD's[3] monograph on the water lilies. The differences of opinion as to certain characters of the embryo, expressed by CONARD on the one side and LYON and myself on the other, led me to believe that the embryological characters are subject to considerable variation, or that some serious error had been made. However, I determined to verify my work on *Castalia odorata* and *Nymphaea advena*, if possible, and YORK's[4] work on Nelumbo. Recently SEATON[5] has published a paper on *Nymphaea advena*, which also deserves consideration in this review of the subject.

My recent studies have been confined to the disputed points in *Castalia odorata*, *Nymphaea advena*, and *Nelumbo lutea*, and therefore other species and other questions have been given very little or no consideration.

EMBRYO SAC

The mature embryo sac is subject to considerable variation. However, I am now convinced that the formation of a cross-wall between the two daughter nuclei, which are formed by the first division of the endosperm nucleus, is a constant character, although SEATON failed to find it in *Nymphaea advena*. It is usually very delicate and is no doubt frequently

[1] LYON, H. L., Preliminary note on the embryogeny of Nelumbo. Science N. S. **13**:470. 1900.

———, Observations on the embryogeny of Nelumbo. Minn. Bot. Stud. **2**:643–655. 1901.

[2] COOK, M. T., Development of the embryo sac and embryos of *Castalia odorata* and *Nymphaea advena*. Bull. Torr. Bot. Club **29**:211–220. 1902.

[3] CONARD, H. S., The water lilies: a monograph of the genus Nymphaea. Carnegie Inst. Wash. Publ. 4. 1905.

COOK, M. T., The embryology of some Cuban Nymphaeaceae. BOT. GAZETTE **42**:376–392. 1906.

[4] YORK, H. H., The embryo sac and embryo of Nelumbo. Ohio Nat. **4**:167–176. 1904.

[5] SEATON, SARA, The development of the embryo-sac of *Nymphaea advena*. Bull. Torr. Bot. Club **35**:283–290. 1908.

destroyed in the preparation of the material. The writer has observed it repeatedly in *Castalia odorata* and in *Nymphaea advena*, where it can be seen without great difficulty; also in *Cabomba piauhiensis* and in *Brasenia purpurea*, where it is very difficult to demonstrate. YORK noted it in *Nelumbo lutea*, but according to his observations one of these two cells again divides, thus forming three superposed cells, each of which is active in the formation of the endosperm. However, he did not observe the formation of the large vesicular cell, which is so characteristic of the other genera of this family. My recent studies, which will be referred to later in this paper, do not fully agree with those of YORK in regard to the vesicular cell.

The daughter nucleus in the micropylar end of the sac always divides to form the endosperm. The formation of the nucellar tube, into which the other nucleus usually and possibly always passes, is subject to considerable variation in the different species. In the genus Nymphaea it is a cylindrical tube, which extends almost the entire length of the ovule (*fig. 1*). In Castalia it may be in the form of a tube which is practically the same as in Nymphaea, but it is usually somewhat shorter and narrower. In some of my recent studies I have found individuals in which there were well-formed tubes extending only about one-half the length of the ovule (*fig. 2*), while in other individuals it extended not more than one-third the length of the ovule and tapered to a point (*fig. 3*). In *Castalia ampla*, as previously reported by me, it develops into a short, sac-like structure (*fig. 4*), which is eventually overgrown by the micropylar part of the sac (*fig. 5*). In *Brasenia purpurea* and *Cabomba piauhiensis*, the tube is very long, extending almost the entire length of the ovule, and very small (*fig. 6*). In *Nelumbo lutea*, according to these studies, the tube is very irregular in form and extends about two-thirds the length of the ovule (*fig. 7*).

In these recent studies one individual of *Nelumbo lutea* was observed in which two sacs were formed one below the other in the main axis of the ovule (*fig. 8*). The antipodal ends were in contact, and the sac next to the micropyle was about four times as large as the other. It showed a fully developed egg-apparatus, and the two polar nuclei were in contact, but the antipodals had disintegrated. The small sac which was farthest from the micropyle showed the egg, one synergid, the three antipodals, and was filled with the characteristic endosperm. In the antipodal end of the sac was a small, deeply colored mass, which was possibly the remains of the disintegrating tube nucleus (*fig. 8 t*). This extra sac was evidently derived from one of the sister megaspores. YORK observed many cases in which extra, imperfect sacs were produced, and expressed the opinion that they were from sister megaspores rather than from independent mega-

sporocytes. I have previously recorded the occurrence of extra, imperfect sacs in Castalia, Brasenia, and Cabomba, but in all cases I considered them to have been derived from independent archesporial cells. In this new case, to which I now refer, it was evident that the second sac had not been penetrated by a pollen tube, and of course the endosperm had been formed without triple fusion. In this connection I wish to say that I have previously observed sacs of species of this family which were filled with typical endosperm, but without embryos, and in which it appeared that there had been no fertilization.

However, in the normal embryo sacs of *Nelumbo lutea*, the polar nuclei united in the usual manner and then divided to form the endosperm. I was unable to follow the early divisions of the endosperm, but in a few instances I found a well-marked cell wall across the sac, which I take to be the wall that is usually formed between the two daughter nuclei after the first division of the endosperm (*fig. 10*). The tube nucleus (*t*) was comparatively small and undergoing disintegration. The antipodal end of the sac is in contact with an axial mass of cells (*fig. 11*), which may consist of a single row of cells or many rows. These cells are rich in protoplasm and eventually disintegrate, probably forming food for the developing embryo. They have been referred to by YORK, who gave a discussion of their appearance and behavior, and figured them in his paper. They are very similar to the cells in the secondary sac (*fig. 8*), and I am inclined to consider them as the vestiges of undeveloped embryo sacs. Near the cross-wall, but in the micropylar chamber of the sac shown in *fig. 10*, was a rather compact mass of cells (*d*), which somewhat resembles a second embryo, but a careful examination leads me to believe it a part of the endosperm.

In one ovule of *Castalia odorata* the embryo was well advanced, although the endosperm nucleus had remained undivided (*fig. 13*).

EMBRYOS

In my first paper I stated that the embryos are without suspensor, except in the case of *Nymphaea advena*, in which a latent suspensor is developed. CONARD afterward described and figured a suspensor for Castalia. In a more recent paper on the Cuban forms, I described the embryo of *Nymphaea advena* as developing in the same manner as our northern form, except that the latent suspensor was more prominent in the Cuban form. However, the embryos of *Castalia ampla* and *C. pubescens* develop with filamentous suspensors in the manner described by CONARD for *Castalia odorata*, while Cabomba and Brasenia both develop with short fila-

mentous suspensors. SEATON'S observations on the embryo of *Nymphaea advena* coincided with my first paper on this subject.

In these later studies I have found that the embryo of *Nymphaea advena* originated (*fig. 12*) and develops in the same manner as previously described by me, but that in some instances the latent suspensor is almost or quite as prominent as in the Cuban form. In *Castalia odorata* I found both types of embryos described by me in my first paper; i. e., without a suspensor (*fig. 13*), and also with a suspensor (*fig. 14*), as described by CONARD and by myself in my paper on the Cuban Nymphaeaceae. These recent studies on *Nelumbo lutea* showed in most cases a spherical embryo, without a suspensor, and agreed fully with the observations of LYON and YORK, but in one or two cases there appeared a small suspensor (*fig. 10*) of the same type as described for *Nymphaea advena*, except that it appeared somewhat earlier in the development of the embryo.

Recent studies on *Castalia odorata* and *Nymphaea advena* confirm the previous observations of myself and others on the formation of a cotyledonary ridge, from which the two cotyledonary lobes are developed.

The studies referred to in this paper convince me that the species of Nymphaeaceae are either very plastic and subject to considerable variation, or that we are confusing very closely related forms.

SUMMARY

1. Extra embryo sacs are frequently formed.

2. The cross-wall between the two daughter nuclei, which are formed by the first division of the endosperm nuleus, is usually present, although so delicate that it is very difficult to demonstrate.

3. The nucleus in the micropylar end of the sac forms the endosperm.

4. The nucellar tube is somewhat different in the different species, and also subject to great variation, especially within the genus Castalia.

5. The embryo of Nymphaea originates without a suspensor and later develops a latent suspensor; the embryo of Castalia originates either without or with a filamentous suspensor; the embryos of Cabomba and Brasenia with short filamentous suspensors; and the embryo of Nelumbo either with or without the very short latent suspensor.—MEL. T. COOK, *Delaware Agricultural Experiment Station, Newark, Delaware.*

EXPLANATION OF PLATE VI

Abbreviations: *e* embryo; *t* tube nucleus; *n* egg; *s* synergids: *a* antipodals; *w* cross-wall.

FIGS. 1–7.—Diagrams of ovules, showing sac and nucellar tube: *fig. 1, Nymphaea advena; figs. 2, 3, Castalia odorata; figs. 4, 5, Castalia ampla; fig. 6,* Brasenia and Cabomba; *fig. 7, Nelumbo lutea.*

FIG. 8.—Two embryo sacs in axillary order; the one next to the micropyle is the larger.

FIG. 9.—Embryo sac of *Nelumbo lutea*, showing egg apparatus and endosperm nucleus.

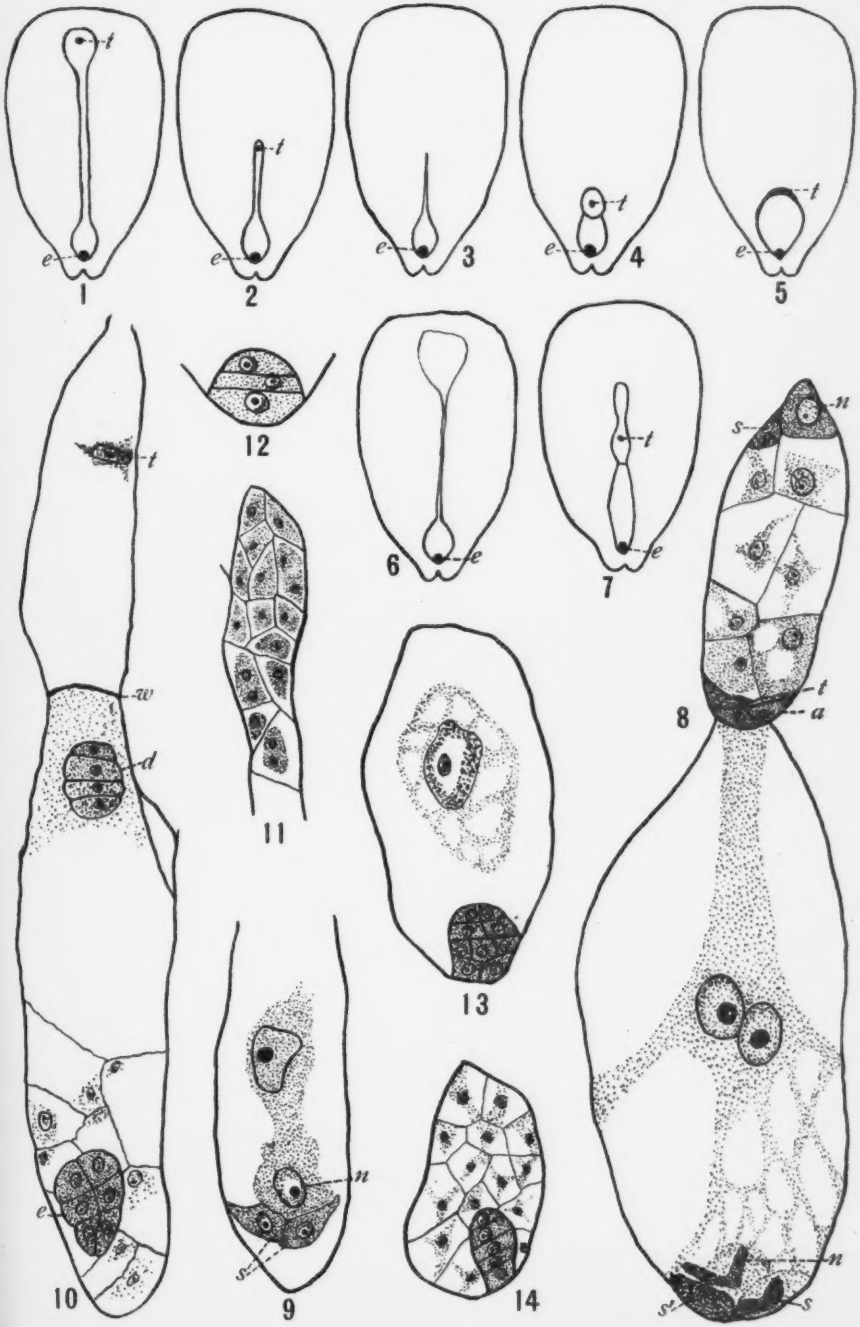
FIG. 10.—Embryo sac of *Nelumbo lutea*, showing embryo, cross-wall, and disentegrating tube nucleus.

FIG. 11.—Cells from the axial region of the ovule which may be the endosperm of unfertilized embryo sacs; from same section as *fig. 10*.

FIG. 12.—Embryo of *Nymphaea advena*.

FIG. 13.—Embryo of *Castalia odorata* and sac with the undivided endosperm nucleus; embryo without suspensor.

FIG. 14.—Embryo of *Castalia odorata* with suspensor.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CURRENT LITERATURE

BOOK REVIEWS

Mendelism

A book by BATESON entitled *Mendel's principles of heredity*[1] has recently appeared from the Cambridge Press. The work is divided into two parts. The first part is a compilation and summary of all Mendelian work to date. The second part contains a biographical sketch of MENDEL and a translation of his two classic papers on hybridization in Pisum and Hieracium. The latter also appeared in the celebrated *Defense of Mendel*, published by the same author in 1902.

The body of the work is occupied with an account of the facts of Mendelian inheritance, as they have been accumulated since the work of MENDEL was brought to the attention of the scientific world at the beginning of the century; and a considerable proportion of this work is the result of the activities of BATESON and his students. The first three chapters contain the principles of Mendelian theory, as they have been developed and modified. The next five chapters deal with the phenomena of color heredity, indicating the prominent place the study of color characters occupies in Mendelian literature. The phenomena of "gametic coupling" and "spurious allelomorphism" are described and explanations suggested. Other chapters are concerned with heredity and sex; Mendelian inheritance in man; intermediates between varieties; Mendelian conceptions of the nature of units; the nature of segregation, reversion, variation, etc.; and the final chapter of part I is devoted to the practical application of Mendelian principles. The last chapter will prove useful to practical breeders of plants and animals, for even if there is not an *actual* segregation of characters, it is undeniably true that in many cases characters *behave as though* a segregation and recombination according to chance had taken place. There are certain cases, however, in which it is very difficult to suppose that a segregation takes place at the time of chromosome reduction. Such a case is that of two white races of sweet pea, one having long pollen and the other round. In the F_1 of this cross all the hybrids have long pollen, while if a segregation of characters had taken place during reduction, we should expect to find in each tetrad of pollen grains two long and two round.

The general aspects of Mendelian theory are but lightly touched upon in this work, since the author intends to deal with these in a separate volume. The remarks on every page, however, as well as the brief discussion of these topics leave no doubt as to the interpretation placed upon the phenomena described. It

[1] BATESON, W., MENDEL'S principles of heredity. 8vo. pp. xvi+396. *pls. 6*, colored. *pls. 3*, half-tone portraits of Mendel. *figs. 37*. Cambridge: University Press; New York: G. P. Putnam's Sons. 1909. $3.50.

is a curious blindness to other facts of heredity which leads the author to the opinion that Mendelism probably represents the only type of inheritance which exists. Because characters sometimes behave as units does not exclude the occurrence of several other types of hereditary behavior, nor does the recognition of this fact belittle the facts of Mendelism. In the comparison of GALTON's law of ancestral inheritance with the Mendelian ratios, the fact that GALTON's law was designed for populations rather than for individuals seems to have been overlooked.

The method by which the process of segregation is visualized is very well exemplified in the following quotation (p. 56):

> Henceforth we have to penetrate behind the visible appearance of the individual, and endeavor to reconstruct first those processes of cell division which produced the germ-cells or gametes, distributing the characters or factors among them according to definite systems; and then the subsequent process of union of those gametes, pair by pair, in fertilization to form zygotes, each developing and manifesting in its development those properties of structure, instinct, and conduct conferred upon it by that particular complement of factors which its two original gametes contained.

Yet, fascinating as the theory appears, it must be remembered that it still remains an unproven hypothesis, to explain a characteristic method of hereditary behavior. The hypothesis has certainly proved useful, even though another explanation of the phenomena of segregation may ultimately be found necessary.

The book is attractively printed on a good quality of smooth paper, and appears to be exceptionally free from typographical errors. Its attractiveness is enhanced by three photographs of MENDEL and several colored plates, together with numerous illustrations and diagrams. A bibliography, and subject and author indices are found at the end of the volume. The work will be indispensable for reference by all students of heredity as a compendium of Mendelian phenomena.

A small volume entitled *Mendelism*, by R. C. PUNNETT, a collaborator with BATESON, was published in 1905 and passed through a second edition. An American edition[2] has just appeared, with a preface by GAYLORD WILSHIRE. It is a simple, clear account of Mendelian phenomena, and as such has doubtless done much to popularize Mendelism among general readers. The new edition also contains reprints of an article on "Applied heredity," which appeared in *Harper's Monthly Magazine*, and an article subtitled "Old Bottles," reprinted from *The New Quarterly*, which is chiefly a criticism of THOMSON's volume on *Heredity*,[3] of the position taken by WALLACE and POULTON, and the attempt to minimize the importance of non-Mendelian types of inheritance. The paper is poor and the diagrams coarse, but the little book will doubtless serve its purpose as a cheap and popular presentation of Mendelism.—R. R. GATES.

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[2] PUNNETT, R. C., Mendelism. 12mo. pp. 109. New York: Wilshire Book Company, 200 William St. 1909. 50 cents.

[3] THOMSON, J. ARTHUR, Heredity. London. 1908.

The determination of sex

STRASBURGER's latest work deals with the time of the determination of sex, apogamy, parthenogenesis, and the reduction division.[4]

The discussion in regard to the determination of sex is based largely upon the behavior of the spores of the dioecious liverwort Sphaerocarpus. Two spores of a tetrad give rise to male plants and the other two give rise to females. The conclusion is that the sex tendencies are separated during the two mitoses by which the four spores are formed from a mother cell. In the homosporous pteridophytes with monoecious prothallia, the expression of the sex tendency, as shown by the formation of antheridia and archegonia, does not take place so early, and in heterosporous pteridophytes all the spores of a tetrad, and even of a sporangium, produce plants of one sex. This is true also of spermatophytes, all of which have strictly dioecious gametophytes. STRASBURGER concludes, as had also CORRENS and NOLL, that the egg tends to produce females, and he believes that the mitoses in the pollen mother cell separate male tendencies of unequal vigor, so that, in dioecious plants, two microspores of a tetrad will give rise to sperms, which, in fertilizing the egg, are prepotent over the female tendency and so will produce males. The other two microspores of the tetrad will give rise to sperms which are not able to overcome the female tendency of the egg, and hence it will produce females. The hybrid obtained by pollinating *Fragaria virginica* with the pollen of *F. elatior* has been explained as a case of merogeny, but STRASBURGER found that fertilization occurs regularly, and that both male and female plants are produced. All the plants, however, resemble the male. This shows that the heritable characters of one of the nuclei which unite in fertilization can dominate the other. There is, as yet, no cytological evidence of the separation of sex-determining structures in plants.

Aside from a critical review of the literature, the discussion of apogamy is based principally upon an investigation of *Wikstroemia indica*, and 62 of the 88 figures illustrate critical stages in the life-history of this plant. As in other apogamous forms, the chromosome number is higher than in normal related species. In the pollen mother cells the mitoses differ from those of normal plants, and pollen tubes are never formed. The first mitosis in the megaspore mother cell shows some abnormalities. A wall is formed between the two daughter nuclei, but at the next mitosis, which usually occurs only in the lower cell, no wall is formed. An eight-nucleate embryo sac with a $2x$ egg is formed from the lower cell, and from this egg the $2x$ embryo is formed without fertilization. STRASBURGER regards this as a case of apogamy (*Eiapogamie*), and would reserve the term parthenogenesis for the development of an embryo from an egg with the reduced number of chromosomes. The reason for the discrimination is that he regards the $2x$ eggs as practically already fertilized.

[4] STRASBURGER, EDUARD, Zeitpunkt der Bestimmung des Geschlechts, Apogamie, Parthenogenesis und Reduktionsteilung. Histologische Beitrage VII. 8vo. pp. xvi + 124. *pls. 1–3.* Jena: Gustav Fischer. 1909. *M.* 6.50.

In the heterotypic mitosis STRASBURGER interprets the double condition as a parallel conjugation and not as an early splitting, and in this parallel conjugation he finds the explanation of the reduction from the $2x$ to the x number of chromosomes. *Galtonia candicans* furnishes particularly strong evidence that there is a pairing rather than a splitting.

STRASBURGER was one of the first to claim that the nucleus is the physical basis of heredity. Since it has been urged that other structures are concerned, the sperm nuclei of Lilium were carefully reexamined, and it was found that only the nucleus, with no trace of cytoplasm from the pollen tube, enters the egg.

The book closes with some interesting suggestions in regard to the origin and development of the nucleus: The original protoplasm had no nuclei, all its parts being capable of both formative and nutritive functions. Then there was a gradual separation of formative and nutritive parts, and the formative parts were the first differentiated carriers of hereditary qualities. At first they were scattered in the cytoplasm, but later became grouped, as in the Cyanophyceae. Next the nucleus would be marked off from the cytoplasm by a membrane. Simple constriction might suffice for the division of such a nucleus, but as the difference between hereditary units became so great that each unit carried only one quality, a more exact division would become necessary. The units would become arranged longitudinally in a thread, where they would undergo a doubling, and the longitudinal division of the thread would separate the product of that doubling. The complete resemblance between the mitoses of higher plants and animals makes this sequence very probable.

The book touches upon almost every phase of cytological investigation and consequently only a few of its more important features can be mentioned in a review.—CHARLES J. CHAMBERLAIN.

Biology of chlorophyll

Starting from the complementary colors of marine algae, an accepted adaptation to the light at varying depths, as suggested by ENGLEMANN (1883), and the complementary tints attained promptly by certain Oscillatoriae, when exposed to light of differing hues, as shown by GAIDUKOW (1902), STAHL proposes to inquire[5] why plants are green and not some other color, and whether the green of land and water plants is not an adaptation to the composition of sunlight, modified by its passage through the atmosphere. Citing the results of physical investigations to show that in diffuse light the blue and violet rays prevail, and in direct sunlight the red and yellow, he claims that an unrecognized relation exists between these facts and the selective absorption of the chlorophyll. The yellow component serves to absorb the blue-violet; the green component the red-yellow. The yellow pigment is complementary to the blue of the sky, and the green to the red-yellow rays which pass through an atmosphere whose haziness becomes evident to our

[5] STAHL, ERNST, Zur Biologie des Chlorophylls: Laubfarbe und Himmelslicht: Vergilbung und Etiolement. 8vo. pp. vi+154. *pl.* 1. Jena: Gustav Fischer. 1909. *M* 4.

eyes when the sun is low. As the red Florideae are colored in complement to the green-blue rays least weakened by traversing sea water, so the green and yellow of chlorophyll are complementary to the red and blue that traverse the atmospheric sea. It thus appears that the yellowish green of vegetation is really an adaptation to the composition of diffuse light.

Various lines of reflection, more or less closely related to this idea, are elaborated, such as, Regulation of the absorption of the sun's rays; Variable content of chlorophyll in nutritive organs; Biology of non-green algae; Etiolation, autumnal yellowing, and their biological significance.

The book is almost purely philosophical, only a few experiments, and these avowedly superficial, being recorded. Of course the general thesis does not touch the fundamental reason for plant coloration, and it is doubtful whether there is any logical gain in this mode of looking at the facts. To give it validity, it must be shown that the absorption of other rays by different pigments (and consequently a different colored vegetation) would be nutritively inefficient. Considering the fact that most plants get far more energy than they can use at ordinary temperatures, by reason of the inadequate supply of CO_2, it would surely be difficult to show this.—C. R. B.

MINOR NOTICES

Bacterial classification.—JENSEN has attacked the difficult problem of bacterial classification with a view to making a "natural system," that is, one which will express relationship by descent.[6] Most attempts to classify bacteria have been based first upon form or upon mode of cell division, and then upon physiologic characters. This method has led to many anomalies. For example, in one sharply defined family, the red sulfur bacteria, there are found rod, spiral, and round forms; and in the case of certain species of Crenothrix and Azotobacter, division occurs first in one, later in three planes. JENSEN argues that bacteria with a single flagellum, or with tufts of polar flagella, are closely allied, but that these are sharply differentiated in fermentative as well as other reactions from those having flagella distributed over the cell-body. Hence he divides the whole bacterial kingdom into two orders: (1) Cephalotrichinae and (2) Peritrichinae. In the former he groups seven families, in the latter four families. For genera he selects, as a means of discrimination, the oxidizing, reducing, fermentative, and other chemical processes of metabolism, as shown by the work of himself, WINOGRADSKY, BEIJERINCK, KASERER, BURRI and STÜTZER, MOLISCH, OMELIANSKI, BÜCHNER, and others. JENSEN regards the genus Methanomonas as the origin of all organic life, since this autotrophic, monotrichial, rodlike form builds up its cell substance in the simplest manner possible, without requiring either organic carbon, organic nitrogen, or outside energy such as light or heat. On the contrary, a certain

[6] JENSEN, O., Die Hauptlinien des natürlichen Bakteriensystems nebst einer Uebersicht der Gärungsphänomena. 8vo. pp. 42. *fig.* 1. Jena: Gustav Fischer. 1909. *M* 1.

amount of energy is actually set free during the metabolic process of *Methanomonas methanicus*. From this genus evolution progresses in four directions, toward the Protozoa, the Eumycetes, the Cyanophyceae, and toward the putrefying and pathogenic forms. The tree of descent thus outlined is ingenious, and species seem to fall into places of natural relationship. This, however, may only mean that generic distinctions are founded on well-established biological properties, for it is probable that bacteriologists will hesitate to accept a primary division into orders on a basis of the distribution of flagella.—MARY HEFFERAN.

Botanical directory.—A third edition of DÖRFLER'S *Adressbuch* was issued some months ago.[7] It is needless to commend this useful volume to those who know the earlier editions; but we do a real service to any who do not by directing their attention to the greatly improved third edition. The list of botanists with their addresses and specialties is of course the main feature; but very useful also are the lists of botanical periodicals and societies.

If any fault is to be found with the directory it is because it includes too much rather than too little. For example, we would have spared gladly the 270 pages of so-called "bibliography"—really a trade catalogue; but perhaps the author, who is also the publisher, could not afford (financially) to leave it out.

Further, there are too many names included. How to sift the real botanists from the tradesmen and notoriety seekers is a difficult problem; for some of our best-known but heedless botanists have not responded to the circulars of the editor, and many of the sham botanists have. Judging by the United States list the numbers might be reduced 50 per cent., for everybody knows that there are not in this country half of the 1800 listed who ought to be in a botanists' directory. We may suggest to the author the possibility of securing the cooperation of one or more editors in each country to purge the list. Why would not the issuance of this directory as an annual be a good work for the *Association internationale des botanistes?* Certainly it cannot be much of a money-making venture, and no doubt the editor would be glad of support. He is certainly entitled to great credit for the labor he has expended and the risk he has assumed in issuing this indispensable volume.—C. R. B.

Mechanics of plants.—Those who desire a compact and authoritative statement of SCHWENDENER'S present views on the mechanics of plants, as set forth in a course of special lectures given regularly for advanced students in the summer semester at Berlin, will find them in a thin volume[8] recently published by Profes-

[7] DÖRFLER, J., Botaniker-Adressbuch. Sammlung von Namen und Adressen der lebenden Botaniker aller Länder, der botanischen Gärten und der die Botanik pflegenden Instituten, Gesellschaften und periodischen Publikationen. Dritte neu bearbeitete und vermehrte Auflage. 8vo. pp. viii+450. Wien: The author (III, Barichgasse 36). 1909. $3.35.

[8] HOLTERMANN, CARL, SCHWENDENER'S Vorlesungen über mechanische Probleme der Botanik, gehalten an der Universität Berlin. 8vo. pp. vi+134. With portrait of SCHWENDENER and *90 figs.* Leipzig: Wilhelm Englemann. 1909. *M* 3.60.

sor Dr. HOLTERMANN, a docent in the botanical institute. The work does not profess to be a verbatim report of SCHWENDENER's lectures (which he himself could not make ready for the press), but is an expression of his views, based upon his lectures, published works, and personal communications; and moreover, the book has had his revision. The contents must suffice to show the character of the work: The mechanical system; Theory of phyllotaxy; Ascent of sap; Stomata; Twining; Tension of cortex; Distortion of pith rays by excentric growth; Apparatus for gliding; Turgor movements; Hygroscopic curvatures and torsion.

To have these topics treated clearly and tersely is extremely useful, and Dr. HOLTERMANN's service will be appreciated.—C. R. B.

Pflanzenfamilien.—With the exception of a supplement to the section on lichens, which is in preparation, this monumental work[9] has come to an end with *Lieferung 235*, concluding BROTHERUS' exposition of the mosses. It has been in course of publication since 1887, the last part being issued in March, 1909. The high appreciation of botanists all over the world must be the reward of the distinguished senior editor, ENGLER, whose great plan has been so successfully executed. To the publisher, WILHELM ENGELMANN, also, are due congratulations for his courage in undertaking so huge a work, whose commercial success must have been problematic at the outset, and for his efficiency in the details of publication.—C. R. B.

NOTES FOR STUDENTS

The perithecium of Ascomycetes.—The whole of Vol. X of *Le Botaniste* is devoted to an elaborate paper by DANGEARD[10] on the origin of the perithecium in the Ascomycetes. Pages 1–26 are devoted to a general discussion of the subject, while pp. 27–385 are given over to the description of the individual plants studied. The writer is committed thoroughly to a belief in the autonomous nature of the fungi as a group, and in the derivation of the higher forms from phycomycetous ancestors. He postulates at the outset that the ascus is an organ of the same nature throughout the group; that it had a common origin; and that the slight variations which appear are the results of adaptation. He is confronted with four diverse opinions regarding the nature of the ascus: (1) that it is a modified sporangium; (2) that it is a sporocarp or part of a sporocarp; (3) that it is a mother cell presenting special characters; and (4) that it is a sporogonium. Each one of these theories is then discussed. The first, which is that of BREFELD, regards the ascus as a sporangium in which the form has become fixed and the number of spores definite. This is held to be untenable, since it implies the complete absence

[9] ENGLER UND PRANTL, Die natürlichen Pflanzenfamilien, etc. 234 und 235 Lieferung. Brachytheciaceae (Schluss), Hypnodendraceae. Nachträge und Verbesserungen. Von V. F. BROTHERUS. Teil I. Abt. 3. pp. 1153–1246. Leipzig: Wilhelm Engelmann. 1909. *M* 3.

[10] DANGEARD, P. A., L'origine du périthèce chez les Ascomycètes. Le Botaniste 10:1–385. *pls. 1–91.* 1907.

of sexuality in the Ascomycetes, and that the phycomycetous ancestors have transmitted to the higher fungi only the asexual stage. Since asexual conidiophores are numerous in the Ascomycetes, the primitive aerial sporangium must have developed along two different lines, giving rise on the one hand to the ascus and on the other to the conidiophore.

According to the second theory, that of DE BARY, the ascus is either the whole or part of a multicellular structure, the sporocarp, which is the product of the fertilization of an archicarp. The latter is a cell capable of being fertilized, and finds its homologue in the receiving gamete of the alga, bryophyte, or fern. The sporocarp corresponds, therefore, to the oospore or zygospore of the green alga, the sporogonium of the bryophyte, or the leafy plant of the fern. In other words, it is the sporophyte. If all the Ascomycetes developed their asci in the manner of *Dipodascus* or *Eremascus*, this conception of the organ as a sporogonium or sporophyte would hold true, since in these plants the ascus arises directly from the fertilized egg. But DE BARY believed that in the greater number of the Ascomycetes the archicarp gives rise to the whole perithecium, so that the ascus in these cases is not an entire sporogonium but only a part of it, and he regarded it as the equivalent of the spore mother cells in the bryophyte or fern. But it would be remarkable if an organ of such uniform structure should correspond in some cases to a whole sporogonium, and in others to a mother cell only; and DE BARY was in error in thinking that it could be either one or the other according to circumstances.

As to the third theory, the author remarks that, however strange it may seem to homologize asci with spore mother cells, it must be admitted that a certain analogy exists in the limited number of divisions in the ascus to form the spores. If the whole perithecium really arose from the fertilization of an egg, no serious objection could be urged against this homology. But the fruiting body of the Ascomycetes has a mixed origin, since part of the envelope is formed from filaments of the gametophyte. The following additional facts are regarded as antagonistic to this view: (1) In the small number of genera in which the gametangia are still functional, the egg gives rise directly to the ascus, as in *Dipodascus;* (2) in the other genera the gametangia are no longer functional, and the perithecium does not develop from the egg; (3) the formation of the ascus is always preceded by a fusion of nuclei, and no case is known in which the formation of mother cells is preceded or accompanied by a phenomenon of this kind; (4) in the lower siphonaceous fungi, from which the Ascomycetes have arisen, there is no organ which corresponds to mother cells, but one finds on the contrary the sporogonium (oospore, etc.), which is evidently the ancestor of the ascus.

Much discussion is devoted to HARPER'S contention that the fusion of nuclei which precedes the formation of the ascus is without sexual significance. Three points are considered in this connection: (1) the binucleate structure of the ascus; (2) the fusion of the two nuclei into one; (3) the reduction in the number of chromosomes. Against HARPER'S contention, that the binucleate condition of the ascogenous cells is the result of the stimulus of excessive nutriment, it is urged

that the rôle of nutrition is secondary in nuclear division; that more importance should be attached to the proportion of carbon compounds in the protoplasm and to tendencies transmitted from ancestral forms; and that the constant occurrence of two nuclei has more than a nutritive significance. Their fusion must be regarded as of a sexual nature because of the fusion of two energids into one; because the result of the fusion is a sporogonium as in the case of the ordinary egg; because nuclear fusion necessitates a reduction of chromosomes; and because the formation of gametes on the gametophore recalls exactly the transformation of sporangia into conidiophores and has the same cause.

The author believes that the nuclear fusion in asci and basidia really represents the sexual reproduction in the higher fungi, and that the fourth theory mentioned is the true one, viz., that the ascus is a true sporogonium in all species and is therefore sporophytic in its nature. He believes that the primitive ancestral phycomycete had a greater or less resemblance to *Myzocytium vermicolum*. It possessed a thallus bearing sporangia, which, in his opinion, represented the sporophytic stage. The sporangia were very susceptible to external conditions. This was followed by a thallus bearing gametangia, the gametophyte; the fused gametes gave rise to the fertilized egg, which on germination produced a new sporangium or *sporogonium* with the characters of an ordinary sporangium, but with the doubled nuclei. This sporangium was but slightly susceptible to external conditions. The author believes that this point should be strongly insisted upon, that the ancestral type possessed two sorts of sporangia: the one responsive to environment has given rise, under the influence of aerial life, to the various types of conidiophores met with in the Ascomycetes; the other, of sexual origin, has been modified but little and has given rise to the ascus.

The author proposes a new classification of the Ascomycetes, based on the reproductive organs, in which the whole group is divided into two, the *Gamétangiées* and *Gamétophorées*. The first possesses functional gametangia and includes *Dipodascus* and *Eremascus*. In the second the gametangia, if present, are no longer functional, and their place is taken by gametophores.

About forty-five different types of Ascomycetes are described and figured in the major portion of the paper. One cannot but marvel that a single investigator could have found time to study all these forms in detail and with thoroughness. A most confusing use of terms makes the whole discussion difficult to follow.—ELIAS J. DURAND.

Algal-animal symbiosis.—KEEBLE,[11] continuing his interesting experimental investigation of the associations of unicellular algae with the low animals occurring on the larger seaweeds living between and just below the tide-limits on the north coast of France, now reports the occurrence of a unicellular brown alga in *Convoluta paradoxa*, a tubellarian. He had previously found a green Chlamydomonas-

[11] KEEBLE, F., The yellow-brown cells of *Convoluta paradoxa*. Quart. Journ. Micros. Sci. **52**:431–479. 1908.

like alga in another species of Convoluta.[12] The color of the animal is due in part to orange-red glands in the superficial tissues, and in part to yellow-brown algal cells in the deeper tissues as well. The animals appear always to contain these yellow-brown cells, and in attempted cultures of the animals from the eggs, under conditions precluding infection by algae, the animals fail to develop. Furthermore, when older animals, already containing numerous yellow-brown cells, are kept in the dark, the yellow-brown cells disappear, apparently being gradually reduced to indigestible granular remnants. Such animals, again lighted, fail to develop further unless reinfected; then, however, they grow rapidly as soon as the new algae have sufficiently multiplied.

These facts indicate a dependence on the part of the animal upon its algal associates which may well be called parasitism, a degree of parasitism carried to the extreme of consuming the algae only when starvation impends, and under normal conditions falling far short of such destruction. In describing such an association as this, in which one animal becomes parasitic upon many much smaller algae inclosed within its own tissues, our usual vocabulary suffers strain, for words have to be used with altered meanings. Thus we should naturally speak of the animal being infected by the algae, and wonder how it is accomplished; but shall we speak of the infection of a parasite by its host? The relation of host and parasite in these tubellarians is like that of alga and fungus in lichens, the parasite incloses, lodges, and in time of hunger may ultimately devour its host. These convolutas secure their hosts by ingesting them with other food. The animal feeds voraciously on a varied diet. Apparently in these animals, as in many others, digestion of great quantities of food is less complete than when only smaller quantities are taken at once. The brown algae, if ingested in small quantity, are all digested and destroyed, but if the quantity of food is large, some cells escape digestion, entering the tissue of the animal and in a way becoming a part of it.

KEEBLE sees in the photosynthetic activity of these algal cells their value to the animals. The unicellular brown algae contain chromatophores in which there are two pigments: a yellow, quickly soluble in hot 90 per cent. alcohol and decomposed by hot water (fresh?), and a green, which resembles chlorophyll. The products of photosynthesis KEEBLE says he has not been able to determine, but he regards the fat globules in the cells as the form in which the photosynthate is temporarily stored. These fat globules he has seen migrating from the algal cells into the animal tissues, and their number is directly proportioned to the state of nutrition of the two organisms, being abundant in well-lighted animals immediately after being brought into the laboratory, decreasing under the somewhat unnatural conditions of the laboratory, and disappearing entirely if the cultures are placed in filtered (that is, food-free) sea water in the dark. The synthesis of food from CO_2 and H_2O within its own body, if unaccompanied by deleterious products, is of obvious advantage to an animal. Yet the advantage seems to be less in *Convoluta paradoxa* than the earlier studied *C. roscoffensis*. In the latter, the

[12] See review in BOT. GAZETTE **46**:68. 1908.

animal presently ceases to take food from without, and is nourished entirely by its endophytic algae; in the former, the animal continues to feed throughout its lifetime. For some reason, the parasitism is less complete.

The benefit to an animal in association with a plant is much more obvious than the benefit accruing to the plant. It is customary among naturalists to conceive of every structure, every act, every situation, as useful or advantageous to the organism, or as having been useful or advantageous in the past. Many cases might be cited which stultify such a position, yet KEEBLE seeks to find some value to the independent alga in its association with a dependent animal, and believes that it consists in a "solution of the nitrogen problem—a successful method of obtaining large supplies of nitrogen." This is plausible, and adding a usable nitrogen compound, such as uric acid or potassium nitrate, in due proportions to the food-free filtered water of laboratory cultures, prolongs the life and prosperity of plant and animal alike. But as KEEBLE plainly indicates, this profits individuals, not the species. Ingested algae of a certain sort, escaping digestion and manured with animal wastes, multiply in the tissues of this small animal; they grow and prosper; but beyond the body of the individual animal they do not appear to spread. They do not infect the eggs; they do not escape from the body of convoluta before or after its death; they die with it. Each convoluta larva is separately and freshly "infected" by some of its food which it fails to digest. But although KEEBLE has failed to find the alga in its free form, he believes that it has one, and that the species is continued by those individuals which escape the convolutas. Indeed this belief is inevitable, if the ingested and surviving endophytes produce no successors.

I can do no better than quote KEEBLE's own vigorous summary. "The interpretation of the relation between yellow-brown cell and animal depends on the point of view: From that of the animal it is obligate parasitism. From that of the species 'infecting organism,' it is an insignificant episode, involving the loss of that, probably small, proportion of its numbers which are ingested. From that of the individual ingested yellow-brown cell, it is a solution of the nitrogen problem—a successful method of obtaining large supplies of nitrogen."

Obviously, then, to the species of alga there is no use in the association; to certain individuals, which apparently produce no successors, there may be some advantage. Even if there were no other, I suppose some persons would claim an advantage for the algae which escape digestion and survive in the body of the animal, on the hypothesis that life is better than death!

KEEBLE has not yet succeeded in finding the yellow-brown cells in the free state, in cultivating them free from the animal body, or in identifying them with any now known algae; yet he has no doubt of their being algae. There is little reason either to question his opinion or to doubt his ultimate success in cultivating and identifying them.

The theoretical value and interest of this paper is greatly enhanced by the skill and care of the author as experimenter, writer, and draftsman.—G. J. PEIRCE.

Inheritance of albinism.—BAUR[13] has investigated the cause and inheritance of the white-margined condition found in the leaves of some of the common varieties of pelargonium and other forms. The white region of such leaves is composed of cells having colorless instead of green chromatophores, and the periphery, including the growing points, of such plants is found to be composed of 2 or 3 rows of colorless cells. Green cells are ordinarily descended from green, and white from white.

When reproduced by seed the white-margined forms, since their sexual cells are from the peripheral white region, produce pure white offspring, which, having no chlorophyll, are incapable of growth. The occasional white branches produce pure white offspring; and the green branches produce pure green offspring. From the union of a "white" with a "green" sexual cell three kinds of plants are produced: pure green, which breed true; pure white; and green-white mosaics. It is probable that all belong to the last class, the pure white and green being extreme cases in which one type of cell has displaced the other at an early stage.

In the hybrids which show a mosaic of white and green cells in their cotyledons, if the growing point is situated in a green part, then the plant produces only green parts thereafter; if in a white part, only white will be produced; if on the border between white and green, a *sectorial chimera* will be produced, one side of which will bear only green leaves and the other side only white. The production of a chimera of this sort by grafting was recently described by WINKLER[14] in Solanum.

If the growing point is periclinally divided into green and white cells, then the leaves appearing will have the characteristic white margins. In other words, the white-margined varieties of pelargonium are *periclinal chimeras*, the white and green cells of which are both genetically descended from cells of their own sort.

Islands of white tissue surrounded by green in the young seedlings show that the white cell may originate repeatedly from green cells. BAUR's hypothesis of the origin of these types of cells is that the fertilized egg contains both types of chromatophore, which are distributed chance-wise in subsequent cell divisions. If a daughter cell thus comes to have only colorless chromatophores, then all its descendants will be colorless.

Whether the chromatophores are transmitted through the egg alone, as generally believed, or also through the male cell, BAUR hopes to determine. If the former were the case then a "green" male nucleus, for example, would necessarily be able by its influence to cause the development of green in certain of the chromatophores in a "white" egg. A cytological study, to determine the origin and development of chromatophores in the embryo, and the form in which they may be present in the sexual cells, is greatly needed.—R. R. GATES.

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[13] BAUR, EDWIN, Das Wesen und die Erblichkeitsverhältnisse der "Varietates albomarginatae Hort." von *Pelargonium zonale*. Zeits. Abst. u. Vererbungslehre **1**:330–351. *figs.* 20. 1909.

[14] WINKLER, HANS, Ueber Pfropfbastarde und pflanzliche Chimären. Ber. Deutsch. Bot. Gesells. **25**:568–576. *figs.* 3. 1907. See BOT. GAZETTE **47**:84. 1909.

Centrosomes in Stypocaulon.—Since STRASBURGER and SWINGLE's studies, Stypocaulon, one of the brown algae which bears a conspicuous apical cell, has been considered as showing typical centrosomes in thallophytes. According to their account, the centrosome, single at first, divides into two centers, which become surrounded by astral radiations. SWINGLE also described the kinoplasm as clearly distinct from the trophoplasm, the former being the only part of the cytoplasm concerned in the formation of achromatic spindles.

In GRÉGOIRE's laboratory, ESCOYEZ[15] has recently studied the origin of chromosomes and spindles in the nucleus of the apical cell of this plant, and his conclusion is quite different from that of the authors mentioned above. The résumé of ESCOYEZ's results is as follows: (1) In an apical cell, the chromosomes are formed at the expense of a certain part of the nuclear network, the rest and greater part of which remains unused. (2) A nucleolus does not take part in forming the chromosomes; possibly it may furnish chromatin substance to the forming chromosomes, since it becomes disorganized during the prophase. (3) In the telophase, the chromosomes reconstitute the chromatin network in the usual way; a nucleolus then appears, but not by the confluence of chromosomes. (4) Spindles are probably of cytoplasmic origin. (5) The two asters, whose appearance marks the beginning of prophase, do not result from division of a single aster, but they are formed independently, one after the other. (6) It s impossible to distinguish two elements, such as the kinoplasm and trophoplasm, as interpreted by STRASBURGER. Very likely the central bodies which lie in the center of asters are not true centrosomes in BOVERI's sense. They give no evidence of having the nature of the true centrosomes, but represent only cytoplasmic microsomes.—SHIGÉO YAMANOUCHI.

Temperature of insolated leaves.—SMITH, using the new slender thermojunctions of BLACKMAN and MATTHAEI, has determined the internal temperature attained by leaves placed normal to sunlight at Peradeniya.[16] He finds little difference between thin and fleshy leaves in the final temperature attained, which is some 15° C. above that of the air (25–28°), but the latter are less rapidly heated. In the shade the same leaves are 1°.5 below to 4° above the air temperature. He estimates the cooling due to transpiration at 2°.5, which is incredibly low, considering the energy required to evaporate the water transpired. Breezes, even the most moderate, are the more efficient cooling agents, reducing the temperature by 2°–10°. Red leaves were found to attain higher temperatures than a white or pale leaf of like texture and thickness.

The second part of the paper has little connection with the first. In it SMITH records observations to show that the new growth of a large number of trees

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[15] ESCOYEZ, E., Caryocinèse, centrosome et kinoplasme dans le *Stypocaulon scoparium*. La Cellule **25**: 181–201. *pl. 1.* 1908.

[16] SMITH, A. M., On the internal temperature of leaves (we omit the rest of a five-line title). Annals Roy. Bot. Gard. Peradeniya **4**: 229–298. 1909.

at Peradeniya occurs in the driest part of the year (all of which is very wet). To account for this, he suggests that it is only in the drier period that the transpiration stream can supply enough salts! Then on this assumption he erects another: "If this be the case, the higher internal temperature attained by the coloration of young leaves would promote the some object, viz., the increase of the transpiration stream." All of which is an excellent example of spoiling good observations by bad logic.—C. R. B.

Sex in dioecious plants.—A study of the two mitoses by which the microspores are formed from the mother cell in *Acer negundo* has led DARLING[17] to interpretations and conclusions about which there may be considerable difference of opinion. He finds that all the chromatin of the resting nucleus of the microspore mother cell is contained in the nucleolus. Chromatin from the nucleolus diffuses upon the linin and in this way there is built up a spirem which segments into eight chromosomes. Later, five more chromosomes are formed from the nucleolus, so that, all together, there are thirteen chromosomes formed in these two ways. After the second mitosis, two of the daughter nuclei differ from the other two in containing one more chromatin mass, but when the resting stage is reached, the four nuclei look alike.

The writer believes he has found something somewhat analogous to the maturation mitoses in some insects, and that the peculiarities in *Acer negundo* have some connection with the determination of sex.

The fact that the division of the chromosomes at the second mitosis could not be determined with certainty would indicate that the technic was hardly sufficient to establish the claim that the eight and five chromosomes originate differently. The problem, however, is important and the presentation of results suggestive.—CHARLES J. CHAMBERLAIN.

Chlorophyll of seeds.—MONTEVERDE and LUBIMENKO, working independently, have arrived at the same conclusion regarding the green pigment of the seeds of thirty-eight Cucurbitaceae, viz., that it is not chlorophyll, but that it resembles the protochlorophyll of etiolated leaves.[18] Yet neither in the living nor the dead hulls does it go over, under the influence of light, into chlorophyll. It appears rather late in the development of the seed, in chromatophores which are indistinguishable from chloroplasts and may even contain chlorophyll also. Its absorption spectrum differs in certain details from that of living green leaves. They propose to call this new pigment chlorophyllogen, retaining the name protochlorophyll for the optically altered chlorophyllogen which one can observe in dead tissues and neutral solutions. This chlorophyllogen becomes transformed into chlorophyll under the influence of light plus some other yet unknown factor

[17] DARLING, CHESTER ARTHUR, Sex in dioecious plants. Bull. Torr. Bot. Club 36:177–199. *pls. 12–14.* 1909.

[18] MONTEVERDE, N., UND LUBIMENKO, W., Ueber den grünen Farbstoff der inneren Samenhülle einiger Cucurbitaceen und dessen Beziehung zum Chlorophyll. Bull. Jard. Imp. Bot. St. Petersbourg 9: 27–44. 1909. (Russian: German résumé.)

(possibly an enzyme produced only in light), which is not operative in cucurbitaceous seeds, but is active in etiolated leaves.

Perhaps other so-called chlorophyll originating in the dark will prove to be only this forerunner of chlorophyll. The authors will continue their further researches together. Out of 800 species in 110 families observed, they have found chlorophyllogen in representatives of 18 families.—C. R. B.

Nucleoli in Marsilia.—To prove whether or not there is any transfer of chromatin substance into nucleoli and vice versa, BERGHS[19] has studied vegetative mitosis in the root and prothallium of *Marsilia macra* and *M. Drummondii*. A peculiar condition of the nucleolus in Marsilia was described two years ago by STRASBURGER. The resting nucleus in these species generally contains a single conspicuous nucleolus, which always takes stains deeply, and at a certain stage almost all of the stained substances are found only in the nucleolus. BERGHS, after following the whole processes of vegetative mitosis in the meristem of the root and in the young prothallium, gives the following results. The nucleolus is achromatophile at the moment of its appearance, and afterward becomes more and more chromatophile; at the same time the chromatin network loses its chromatin and decreases in size. The chromatin network in the resting nucleus certainly does not contain the total substance of the definite chromosomes, and in the prophase the nucleolus loses chromatin matter during the formation of chromosomes. The fact that the nucleolus is formed as an achromatic substratum and becomes impregnated with chromatin material during the resting stage, the author believes, indicates a transfer of chromatin material between the nucleolus and chromosomes.—SHIGÉO YAMANOUCHI.

Development of Aeginetia.—The morphology and anatomy of *Aeginetia indica* were described by KUSANO a few years ago, but he found nothing peculiar which would distinguish it from Orobanche. But it does show interesting features in its germination and early growth, which he describes in a recent paper.[20] The short-lived seeds germinate only under stimulation by some substance or substances arising from the roots of vascular plants, and the development of the seedling takes place only on certain species of monocotyledons. The first sign of germination is the appearance of large globular cells at the radicular end of the embryo, from several of which develop hairs, sometimes a millimeter in length, that protrude in all directions. When they come into contact with the host root, they attach themselves (by slight insertion or cement?), and then coil irregularly, thus drawing the embryo close to the host. These tendril-like hairs KUSANO calls hair-tendrils. If the host be suitable the seedling develops a tubercular body, from which arises the primary haustorium. This secures nutriment from the host, making possible later the development of a stem and root system, which arise much as in Orobanche.

[19] BERGHS, J., Les cinèses somatiques dans le Marsilia. La cellule **25**:73–84. *pl. 1.* 1908.

[20] KUSANO, S., Further studies on *Aeginetia indica*. Bull. Coll. Agric. Tokyo Imp. Univ. **8**:1–20 (?). *pl. 7.* 1908.

The stimulus to this development is quite other than that for the hair-tendrils. The latter, according to the author, have not been discovered heretofore in any seed plant.—C. R. B.

Phylogeny of the embryo-sac and double fertilization.—PORSCH [21] attempts to explain the usual eight-nucleate embryo sac of the angiosperms as an extreme reduction from the gymnosperm type, consisting of two reduced archegonia, the egg apparatus and the upper polar nucleus representing one archegonium, and the three antipodals with the lower polar nucleus representing the other. The egg apparatus is regarded as made up of an egg, two neck cells (the synergids), and a ventral canal cell (the upper polar nucleus). The antipodal complex is interpreted in the same way. Then double fertilization might be an attempt to fertilize both archegonia.

While a combination of all the features presented by gymnosperm and angiosperm gametophytes can be arranged in such a sequence, the reviewer does not believe that there is anything phylogenetic in it. Though the angiosperm embryo sac has doubtless come through stages in which there was a tissue with archegonia, we do not believe that any part of the archegonium, except the egg itself, has been retained.—CHARLES J. CHAMBERLAIN.

Chemotaxis of Lycopodium sperms.—BRUCHMANN'S discovery that the sperms of Lycopodium are sensitive to citric acid and its salts is a disturbing factor in SHIBATA'S generalization that the chemotactic sensitiveness of the three great pteridophyte lines toward malic acid approves the theory of their monophyletic origin. Yet BRUCHMANN, apparently not sensing the humor of this idea, gravely softens the blow by suggesting that this aberrant behavior of the Lycopodium sperms does not place the lycopods outside this line of descent, but is to be explained by the saprophytic character of the odd gametophyte![22] He shows that malic acid is not responded to, and that saccharose, glucose, lactose, albumin and other proteins, acetic, oxalic, formic, and butyric acids are likewise ineffective. But to citric acid 1:1,000,000, and to its alkali salts in 1:100,000, the sperms respond positively, the reaction becoming negative at 1:1000 and 1:100 respectively. Acids and alkalies proved repulsive, as in the case of other sperms. The Weber law was found to be valid, with the ratio 1:30–40.—C. R. B.

Geotropic perception.—NEWCOMBE, after criticizing again the weakness of the experiments for the localization of geoperception, has used the old decapitation method for demonstrating that in some species as much as 4 or 5^{mm} of the root tip is capable of perceiving the gravity stimulus.[23] He is unable to relate the

[21] PORSCH, OTTO, Versuch einer phylogenetischen Erklärung des Embryosackes und der doppelten Befruchtung der Angiospermen. Vortrag gehalten auf der 79. Versammlung deutscher Naturforscher und Aertzte in Dresden am 16. Sept. 1907. pp. 1–49. 14 text figures.

[22] BRUCHMANN, H., Von der Chemotaxis der Lycopodium-Spermatozoiden. Flora **99**:193–202. 1909.

[23] NEWCOMBE, F. W., Gravitation sensitiveness not confined to apex of root. Beih. Bot. Centralbl. **24**:96–110. *pl. 3. figs. 6.* 1908.

extent of this region to the length of the elongating zone. PICCARD's method of 1904, which has lately been justified by HABERLANDT,[24] is considered by NEWCOMBE as "too precarious to be satisfactory." All the phenomena, he concludes, "accord equally well with the hypothesis of the extension of the sensitiveness through the elongating zone, but diminishing from the apex backward; or . . . . of a more equable sensitiveness through the elongating zone, and a stronger autotropism in the posterior than in the anterior part." We should much prefer the former hypothesis; if for no other reason, because it is unfortunate to postulate "autotropism" when it can be avoided.—C. R. B.

Development of Marchantia.—Because no consecutive account of the development of the sexual organs and sporogonium of Marchantia, complete in itself, has been published by one author, DURAND, while preparing slides for class use, has published an account of the development illustrated with a close series of figures.[25] The account contributes little which is new to students making a critical study of this form. For the first time, although it has been illustrated by CURTIS, formal attention is called to the familiar "mushroom anchor" foot. One striking feature in the development of the sporophyte has been overlooked: the sterile plate of cells at the apex of the capsule, and also the occasional appearance of a columella, which in some instances extends entirely through the center of the capsule. Because of its relation to the theory of sterilization of sporogenous tissue this plate of cells and the occasional columella should have some attention. —W. J. G. LAND.

The nucleus of bacteria.—MEYER claims[26] that the following methods will differentiate a nucleus in the bacteria. The particular form used was *Bacillus Pasteurianus*. First method: boil in water, stain 24 hours in hematoxylin, and differentiate in weak hydrochloric acid. The nuclei of young spores are sharply outlined. Second method: fix in Flemming's solution, harden in 20 per cent. alcohol, stain in Delafield's hematoxylin, and differentiate with hydrochloric acid. Third method: fix in Flemming's solution, harden in alcohol, stain in iron alum hematoxylin, and differentiate under the cover glass with ammonium ferrosulfate. Judging from the figures, this method gives the best results.

In the opinion of the reviewer, the fact that MEYER does not believe that any nucleus has as yet been demonstrated in the Cyanophyceae would not inspire confidence in his interpretation.—CHARLES J. CHAMBERLAIN.

Anatomy of Sapotaceae.—Incidentally, in seeking the origin of laticiferous tissue in Sapotaceae, Miss SMITH[27] made anatomical studies of seedlings of fourteen

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[24] BOT. GAZETTE **47**:482. 1909.

[25] DURAND, ELIAS J., The development of the sexual organs and sporogonium of *Marchantia polymorpha*. Bull. Torr. Bot. Club **35**:321–335. *pls. 21–25*. 1908.

[26] MEYER, ARTHUR, Der Zellkern der Bakterien. Flora **98**:335–340. *figs. 3*. 1908.

[27] SMITH, WINIFRED, The anatomy of some sapotaceous seedlings. Trans. Linn. Soc. London II. **7**:189–200. *pls. 25, 26*. 1909.

species distributed among eight genera. The vascular system of the primary root and hypocotyl is typically tetrarch and corresponds with two bundles from each cotyledon without change of position. In some species the root is hexarch; in others, variable and anomalous. The occurrence of the hexarch type led the author to suspect that a central cotyledonary trace, such as is found in some species of Diospyros, had aborted, but no sign of this could be found. In *Bumelia tenax* the root is usually hexarch. In the upper part of the root and the hypocotyl, four of these bundles differ from the other two in that from them alone rise the lateral rootlets, and also in that they alone are continuous with the bundles of the cotyledons.—W. J. G. LAND.

Fungus excreta.—A condition almost like that in successive cultures of the higher plants is reported for certain fungi by LUTZ.[28] He finds that in nutritive solutions in which various molds (Aspergillus, Botrytis, Cladosporium, Fusarium, Mucor, Penicillium) have been grown, there are produced substances which retard or accelerate the germination and growth of the same or other species. These products have much in common with enzymes; they are destroyed by high temperatures (80–100° C.); their action is weakened by dilution, ceasing usually at about 20-fold; they are destroyed in sunlight (20 hours), the violet rays being most efficient. Some of these substances may be stopped by a clay filter, but some pass through. The agents which accelerate growth and development are formed in lighted cultures, especially those of Fusarium and Aspergillus.—C. R. B.

Chemotropism of fungi.—As part of the larger subject, parasitism, SCHMIDT has investigated the chemotropism of an unknown species of Phyllosticta, parasitic on pear leaves.[29] He is apparently ignorant of FULTON'S work on this subject,[30] and with experimentation that is open to serious objection, comes to the conclusion that this plant is positively chemotropic. Its chemotropism, however, is not supposed to come into play at once, "but the fungus itself must first, by enzymatic, toxic, or purely mechanical means, so alter the normal structure of the epidermal cell as to set free a diffusion stream, counter to which, as a directive stimulus, the further growth of the fungus proceeds." This view he promises to support in a second paper.—C. R. B.

Culture solutions.—Any who are interested in water-cultures should consult a recent paper by BENECKE,[31] who has been testing the efficiency of VON DER CRONE'S solution, in comparison with the older ones. VON DER CRONE proposed in 1904 a solution nearly like SACHS'S, except in the addition of the iron as ferrous

[28] LUTZ, OTTO, Ueber den Einfluss gebrauchter Nährlösungen auf die Keimung und Entwicklung einiger Schimmelpilze. Ann. Mycol. **7**:91–133. 1909.

[29] SCHMIDT, E. W., Ueber den Parasitismus der Pilze. Zeit. Pflkrankh. **19**:129–143. *figs.* 7. 1908.

[30] BOT. GAZETTE **41**:81–108. 1906.

[31] BENECKE, W., Die von der Cronesche Nährsalzlösung. Zeits. Bot. **1**:235–252. 1909.

phosphate, $Fe_3(PO_4)_2$, instead of the traces of iron which are usually added to the Sachs solution as Fe_2Cl_6. It differs from PFEFFER'S and MAYER'S essentially in the use of tricalcium phosphate, $Ca_3(PO_4)_2$, instead of potassium phosphate, thus avoiding the acidity of these solutions. BENECKE has tested VON DER CRONE'S claims, some of which he finds justified, others not. The details are not of general interest.—C. R. B.

Prochromogens.—In further development of our knowledge of plant chromogens, PALLADIN[32] has found that these substances are not present in any considerable amounts at any time, but that they are formed gradually, from what he proposes to call prochromogens, which there is some ground for thinking are glucosides. These are split up by enzymes and the chromogens are produced in small amounts, except in the spring, when larger amounts may be observed. In dead plants the enzymes give rise to large amounts of the chromogens, because the splitting is then uncoordinated, and the oxidation of these leads to the observed blackening of the tissues.—C. R. B.

Light perception.—Besides the ocelli (in the sense of HABERLANDT), SCHÜRHOFF describes[33] apparatus in six species of Peperomia which may function in the perception of light, namely: the funnelform palisade cells, by reflecting the light to the chloroplasts at their base; the upper convex wall of the palisades, by acting as a lens; and the cluster crystals, that disperse to all the chloroplasts the light focused by the lenticular upper portion of the cell. These ideas seem even more strained than the theory they are adduced to support.—C. R. B.

Wetting of leaves.—AWANO[34] furnishes the ecologists a considerable body of statistics regarding the wetability (there ought to be such a word, if there is not) of leaves. Out of 264 plants examined as to this point, he finds 164, about $\frac{2}{3}$, wetable with difficulty or not at all, while the rest are easily wetable. Leaves of most strand and sand plants are hardly wetable, while those of shade plants and ferns are easily wetable. The details, presented in extensive tables, are combined with observations on the number and distribution of stomata.—C. R. B.

Extrafloral nectaries.—SALISBURY has described[35] the extrafloral nectaries of eight species of the genus Polygonum. He ascribes the secretory action to osmotic pressure of the gland cells, independent of root pressure, and thinks that the nectar glands, which are especially striking in tropical plants, represent originally hydatodes, which have in some cases later acquired a biological significance. He

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[32] PALLADIN, W., Ueber Protochromogene der pflanzlichen Atmungschromogene. Ber. Deutsch. Bot. Gesells. **27**: 101–106. 1909.

[33] SCHÜRHOFF, P., Ozellen und Lichtkondensoren bei einigen Peperomien. Beih. Bot. Centralbl. **23**: 14–26. *pls. 3, 4.* 1908.

[34] AWANO, S., Ueber die Benetzbarkeit der Blätter. Jour. Coll. Sci. Imp. Univ. Tokyo **27**: 1–49. 1909.

[35] SALISBURY, E. J., The extrafloral nectaries of the genus Polygonum. Annals of Botany **23**: 229–242. *pl. 16. figs. 6.* 1909.

finds that there is little reason to suppose that they are of any service in protecting the flowers from ants.—C. R. B.

Centrosomes in Marchantia.[36]—After a study of spermatogenesis in *Marchantia polymorphia*, SCHAFFNER concludes that IKENO's account is correct and that centrosomes are present, both while the nucleus is at rest and while it is undergoing mitosis. His figures are practically the same as IKENO's. MIYAKE's failure to find centrosomes he attributes to differences in technic.—CHARLES J. CHAMBERLAIN.

Thermotropism.—POHL[37] describes observations and experiments that he has made upon the cultivated flax, which show its great sensitiveness to radiant heat, the young shoots directing themselves toward the source. Experiments also show that heat is the dominant factor in inclination of the shoots, which is often ascribed to light.—C. R. B.

Discomycetes.—MISS BACHMAN has published[38] a descriptive catalogue of the Discomycetes within five miles of Oxford, O. Keys to genera and species are provided, and there are illustrations of ten of the sixty-odd species, a goodly number of which are now for the first time reported from southwestern Ohio.—C. R. B.

Light and respiration.—LÖWSCHIN reports[39] that when he excluded the effects of actinic warming he was unable, in the course of twenty-two experiments upon the respiration of certain fungi (Aspergillus, Penicillium, Oidium, and Cladosporium), to detect any regular acceleration of it by light.—C. R. B.

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[36] SCHAFFNER, JOHN H., The centrosomes of *Marchantia polymorphia*. Ohio Naturalist **9**:383–388. *pl. 21*. 1908.

[37] Pohl, J., Der Thermotropismus der Leinpflanze. Beih. Bot. Centralbl. **24**:111–131. *figs. 6*. 1908.

[38] BACHMAN, FREDA M., Discomycetes in the vicinity of Oxford, Ohio. Proc. Ohio State Acad. Sci. **5**:19–70. *pls. 4*. 1909.

[39] LÖWSCHIN, A., Zur Frage über den Einfluss des Lichtes auf die Atmung der niederen Pilze. Beih. Bot. Centralbl. **23**:54–64. 1908.